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CONTRIBUTION TO THE HISTORY OF A MUTATION DURING 1,000,000 YEARS

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INTRODUCTION

This is a report on some results of evolutionary interest that have been obtained in the course of a biometric study of a number of large collections of cave bears (*Ursus spelaeus* Rosenmüller and Heinroth) and brown bears (*Ursus arctos* L.), as well as the ancestral forms, *Ursus etruscus* Cuvier and *Ursus "deningeri"* von Reichenau, in various museums. The main cave bear collections were those from Odessa, now in the Geological Institute of Helsingfors University (collected by Professor Alexander von Nordmann in the 1840's and described by him in 1858–60), and from Mixnitz, now in the Paleontological and Paleobiological Institute of Vienna University (Abel and Kyrle, 1931). The former collection is notable for the great number of isolated teeth, a high percentage being unworn anlages with open roots, which make perfect material for biometric study. Of the recent *U. arctos,* large samples of Finnish, Swedish and Norwegian skulls were available at the Zoological and Anatomical Institutes of Helsingsfors University (abbreviated H.Z.M. and H.A.I. in the text), the Zoological Museum of Copenhagen, the Zoological Institute of Uppsala University, and the Riksmuseum in Stockholm. Other samples, recent and fossil, were studied at the Natural History Museums in Mainz, Wiesbaden, and Leiden, and in the collection of Dr. M. Crusafont, Sabadell.

For details regarding material and procedure the reader will be referred to a more extensive treatment now in preparation. In the present contribution attention will be focussed on a single problem, for which the data at hand are unusually good and which seems to be of general biohistoric interest: the conditions and changes of allometry in the first upper molar of *Ursus arctos* and its subfossil and Pleistocene allies.

CROWN HEIGHT ALLOMETRY IN M^1

In the course of my work it has become clear that allometric [1] relations prevail in bear teeth. The same appears to be true for other mammalian dentitions as well. A number of examples have been gathered in Kurtén (1954 a), where

[1] The allometry concept, fully formulated and exemplified in Huxley's classic treatise (1932), should be well known to all evolutionists.

some procedural concepts are also discussed. An example of dental allometry in phylogeny is given in Kurtén (1954 b). The relation may approach isometry, as in the breadth-length relation of the crown of M^2 in *Ursus* (almost imperceptibly negative allometry, evidently identical for many species of this genus); but well-defined growth gradients are fairly common, as in the case to be considered here.

The samples to be considered initially are as follows:

Ursus arctos, recent (Finland), 40 specimens.
U. arctos, recent (Sweden), 15 specimens.
U. arctos, recent (Norway), 18 specimens.
U. arctos, recent (Pyrenees), 4 specimens (data on 3 kindly supplied by Dr. M. Couturier, Grenoble; the fourth measured from a plate in Couturier (1954)).
U. arctos, recent (various European locs.), 5 specimens.
U. arctos, subfossil (Denmark), 6 specimens.
U. arctos, subfossil (Sweden), 2 specimens.
U. arctos, subfossil (Germany), 1 specimen (data from Soergel (1926)).
U. arctos, latest Pleistocene (Würm Glacial, Ksar Akhil, Lebanon), 2 specimens.
U. arctos, late Pleistocene (Malarnaud, Ariège), 1 specimen (from a plate in Couturier, *op. cit.*).
U. arctos, middle Pleistocene (Choukoutien and other locs., China), 2 specimens.
U. spelaeus, late Pleistocene (Odessa), 94 specimens.
U. spelaeus, late Pleistocene (Schreiberwand Cave, Dachstein, Austria), 15 specimens.

The conditions of allometry in the *Ursus* M^1 appear most clearly in the relations between crown height (expressed as paracone height) and crown length (fig. 1). Paracone height is positively allometric to crown length in both *U. arctos* and *U. spelaeus,* and the trends are seen to be closely similar, but not coincident. The spelaeid relation is more brachyodont, i.e., of two equally long molars the arctoid one would have a considerably higher paracone.

The intrapopulation relationship will express itself in such a way that larger teeth tend to be somewhat more hypsodont than smaller teeth of the same species. (This relation is not valid for all molars. Thus in M^2 there appears to be a negative allometry of height on length, though the deviation from isometry is exceedingly slight.) Side views of small and large first molars for both species are given in figure 2.

The correlation is not, however, absolute; there is a certain scatter around the regression lines. This scatter is summarized for the cave bear in figure 3 and appears to follow the pattern of a normal binomial distribution. On this basis it is possible to determine the standard-range limits of variation away from the regression line. These should be given by lines parallel to the regression line and at a distance of 3.24 σ from it (standard range of Simpson, 1941, giving the probable limits of variation in a sample of 1,000). This distance, in terms of logarithms, was found to be approximately .037 for both *U. arctos* and *U. spelaeus.* (Actually these limits are valid only in the vicinity of the mean, since the error of the coefficient of allometry is not taken into account; but the approximation is useful for the discussion to follow.)

Allometry is genetically determined; it has been found that changes in allometry are heritable and due to mutation. Different allometries, usually more or less parallel, have been found to be allelic with a simple dominant-recessive relationship (Sinnott, 1936).

What, then, about our scatter within the standard limits? Though it might, to some extent, be due to very slight heritable differences in allometry, the nor-

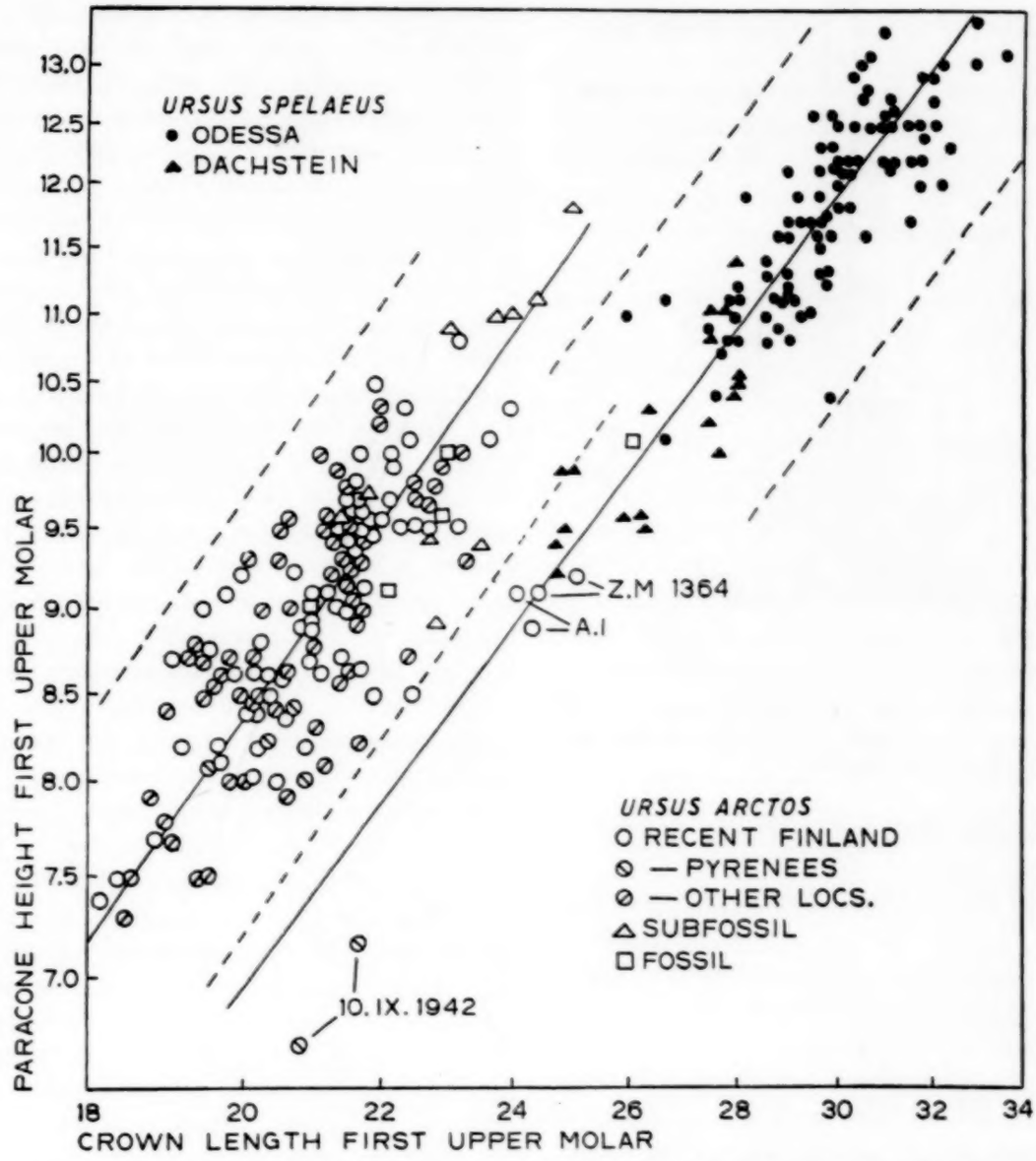

FIG. 1. Logarithmic scatter diagram of paracone height and crown length of first upper molar in recent, subfossil, and fossil brown bears (*Ursus arctos*) and Pleistocene cave bears (*U. spelaeus*) with regression lines and standard-range limits of variation, as defined in the text.

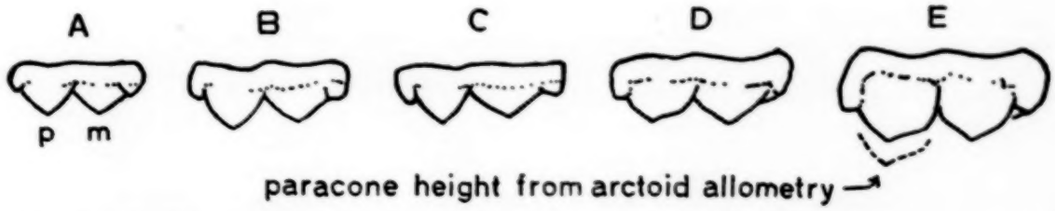

FIG. 2. Outlines of first upper molars in bears, external views; p, paracone, m, metacone. A-B, small and large *Ursus arctos,* recent, Finland; D-E, small and large *U. spelaeus,* Pleistocene, Odessa; C, Z.M. 1364, spelaeid *U. arctos* of recent population (brachyodont). All to scale. Dashed line at E indicates approximate height of paracone that would result from arctoid allometry in a molar of that size.

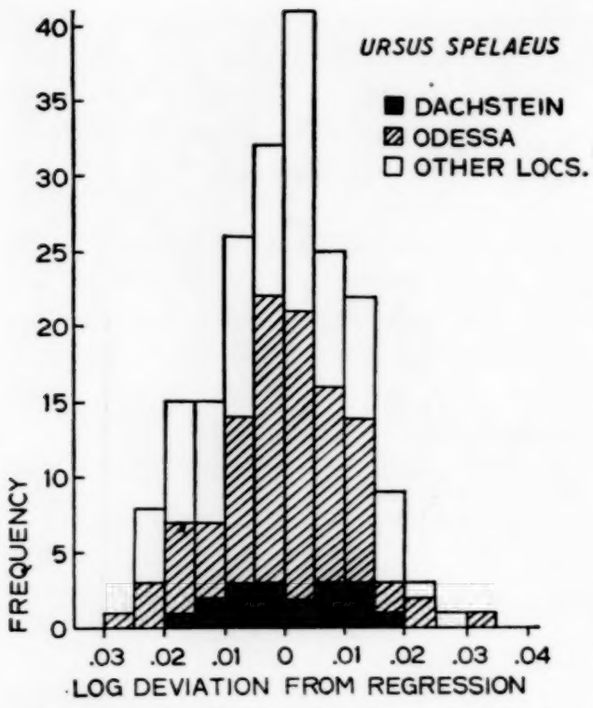

FIG. 3. Distribution around regression line in *Ursus spelaeus*, with contribution of different samples shaded as labelled.

mal pattern of distribution around the regression suggests that it springs, in the main at least, from phenotypic modification. So does the fact that the amount of variation around the regression appears to be fairly constant in different species (see Kurtén, 1954 a).

On the other hand, the sharp difference between *U. arctos* and *U. spelaeus* is doubtless due to genetic change, by means of one or several mutations somewhere in the ancestry of either species or both. The somewhat similar change in allometry in the horse sequence, from tridactyly to monodactyly, was studied by Robb (1936), but as to the number of mutations involved no good evidence could be obtained, the change being poorly recorded in the fossil series. Phleger (1940) observed differences in allometry in felid skulls, that may have been due to mutation, but the evidence is uncertain.

In the present case we have slightly better evidence, some items of which appear from figure 1 (see also figs. 2 and 4). Two of the Finnish *arctos* specimens in my sample (H.Z.M. No. 1364 and H.A.I. without label) are highly aberrant, with remarkably low-crowned first molars. These observations are almost precisely on the extension of the spelaeid regression. The probability for their belonging to the normal distribution in the arctoid sample is so exceedingly low that none of the statistical tables consulted by me bothers about giving the figure. The specimens might be pathological, but there is certainly no evidence for this. Left and right teeth are quite similar in both. H.Z.M. 1364 is a young male, not fully grown and with canines not fully emerged. The H.A.I. specimen is a large subadult male. The cheek teeth are unworn in both. H.Z.M. 1364 was shot in Finland; the H.A.I. specimen is presumably also Finnish in origin. Both specimens are, in addition, characterized by extraordinarily large teeth, in addition to the first upper molar being brachyodont (see table 1).

TABLE 1. *Lengths of tooth crowns in 9 "arctoid" males and 2 "speleaid" males of recent* Ursus arctos *from Finland.* Original data

	"Arctoid"			"Spelaeid"		
	O.R.[a]	M	σ	O.R.	M	M in % of arctoid M
P^4	14.3–18.0	15.83±.43	1.30±.31	17.2–18.4	17.71	112
M^1	20.1–24.0	21.98+.34	1.02±.24	24.1–15.1	24.52	112
M^2	31.1–36.1	33.14±.54	1.52±.38	35.7–39.2	37.97	115
P_4	11.6–14.0	12.68±.30	.89±.21	14.3–14.6	14.47	114
M_1	22.7–25.6	23.65±.33	1.00±.23	24.6–25.0	24.80	105
M_2	22.4–26.5	24.35±.39	1.17±.28	26.2–26.9	26.45	109
M_3	17.8–20.8	19.28±.36	1.08±.25	18.7–23.6	21.18	110

[a] O.R., observed range (limits); M, mean; σ, standard deviation.

A third recent *U. arctos,* from the Pyrenees, also deviates widely from the normal arctoid series, and appears to conform with the spelaeid one. This is the specimen mentioned in the magnificent monograph by Couturier (1954) as "Mâle adulte provenant d'Ossau (Basses-Pyrénées), tué le 10 septembre 1942"; as Dr. Couturier, who kindly sent me the data, informs me, the teeth are completely unworn.

Among fossil and subfossil *U. arctos,* one more spelaeid specimen was encountered in the bear from Malarnaud (see Couturier, 1948 and *op. cit.*).

The variation around the regression line for *U. arctos* (fig. 4) is, therefore, somewhat different in aspect from that of *U. spelaeus.* The distribution is bimodal, with the main part resembling the normal distribution in *U. spelaeus,* but with a secondary mode representing the aberrant specimens. The distributions appear disjunct, but it is of course possible that some of the extreme variants in the normal series actually represent "spelaeids."

Of course these are not instances of "a cave bear tooth in the head of a brown bear"; there are notable differences, for instance in the cusps tapering as in the recent form, not being somewhat truncated as in the cave bear. But in the height-length relation these specimens may be said to "imitate" the cave bear. The conclusion that these are mutants seems to have much to say for it, and

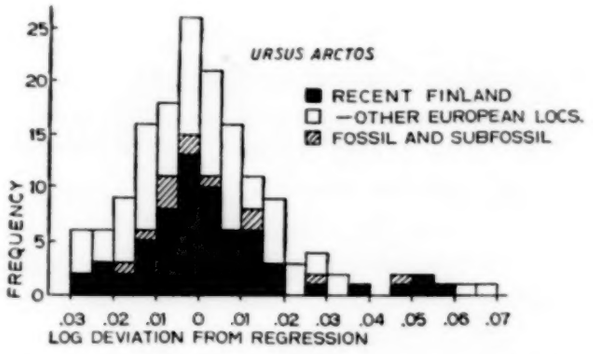

FIG. 4. Distribution around regression line in *Ursus arctos,* with contribution of different samples shaded as labelled. The isolated group to the right represents spelaeid specimens.

this hypothesis raises a number of important questions. Would this be a "new" mutation within *U. arctos,* which happens to imitate *U. spelaeus*? Or would it be an evolutionary "vestige" in the arctoid gene pool, with a line of descent extending back to the common ancestor of the two species? Are the alleles of *U. spelaeus* and the spelaeid *U. arctos* homologous or analogous? How could these data be interpreted in terms of selection?

PHYLOGENY OF THE ALLOMETRY

Additional light is shed on these questions when some other fossil populations are brought into the picture. For a recent account of bear phylogeny, see Erdbrink (1953); I shall here confine myself to short notes on the phyletic position of the samples to be considered below.

Students agree that the cave bear is a descendant of *U. etruscus* from the Villafranchian (basal Pleistocene, according to modern classification; in older work generally placed in the upper Pliocene). An intermediate stage is represented by the middle Pleistocene *U. "deningeri"* (probably to be classed as a subspecies of *U. arctos*). This evolutionary trend (size increase, reduction of premolars, etc.) culminates in the late Pleistocene *U. spelaeus.*

U. arctos also derives from *etruscus,* but whether it descended by way of the European *"deningeri,"* or represents a separate line of descent, is not as yet fully established. In my opinion, there is much to say for the view that the two lines of descent formed a continuous population (and hence a biological species) up to the *"deningeri"* stage, but that most of the heritage of the European *"deningeri"* was passed on to *spelaeus,* whereas the recent *arctos,* in the main, is derived from late Pleistocene immigrants of other local populations.

Besides my own data, I have relied on those published by Soergel (1926). Differences in measuring technique may possibly influence the significance of the com-

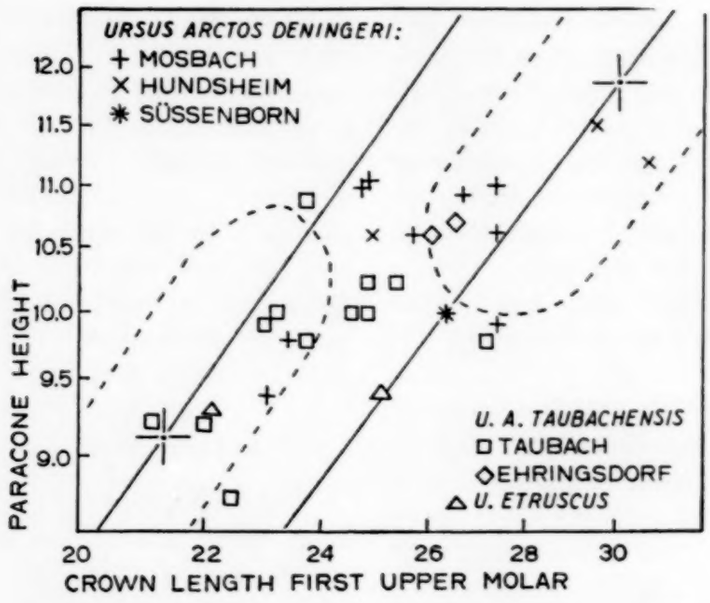

FIG. 5. Logarithmic scatter diagram of paracone height and crown length of first upper molar in Pleistocene bears, as labelled. Data, original and from Soergel. Regression lines from figure 1, with means and limits of observed variations for recent *Ursus arctos* from Finland (left) and Pleistocene *U. spelaeus* from Odessa (right).

parison, but fairly good consistency is indicated. The variates in question are really quite clear-cut, and work by different students should yield comparable results. In the present case, of course, the painstaking precision that characterizes all of Soergel's work would seem to inspire full confidence in his data.

The data pertain to the following samples.

U. etruscus, basal Pleistocene (Val d'Arno, Ronco), 1 specimen.

U. etruscus gombaszögensis Kretzoi, basal Pleistocene (Gombaszög, Hungary), 1 specimen (from Kretzoi's plate).

U. "deningeri," middle Pleistocene (Mosbach sands), 10 specimens.

U. "deningeri hundsheimensis" Zapfe, middle Pleistocene (Hundsheim, Austria), 3 specimens.

U. "süssenbornensis" Soergel (= "deningeri"), middle Pleistocene (Süssenborn, Germany), 1 specimen.

U. arctos taubachensis (Rode), last interglacial (Taubach, Weimar), 12 specimens.

U. arctos taubachensis, last interglacial (Ehringsdorf, Germany), 2 specimens.

As to the phylogenetic significance of these samples, the following opinions may be put down. *U. etruscus* represents the common ancestry of *arctos* and *spelaeus*. The middle Pleistocene *"deningeris"* were ancestral to *spelaeus*. The interglacial *taubachensis* is probably to be placed in close connection with *"deningeri,"* but may have taken some part in the ancestry of the recent *arctos* in the migrations that are to be postulated during the course of the last glacial.

The height-length data are plotted in figure 5, showing the grid of figure 1, with regressions and limits of observed variation for the recent Finnish and Pleistocene Odessan populations.

U. etruscus is represented by two specimens. One (from Ronco) appears to be arctoid, whereas the other (from Gombaszög) shows the spelaeid condition. It may be tentatively concluded that both allometries existed in this early form.

In the relatively large Taubach sample of *U. arctos,* of interglacial date, most intriguing conditions are found. Five specimens (and possibly a sixth) conform perfectly to the normal arctoid pattern of

our recent populations. A single individual shows the typical spelaeid condition, widely diverging from the arctoid regression and closely similar to the two recent specimens from Finland. The remaining 6 or 5 specimens, finally, appear to form a perfectly *intermediate* series totally lacking in most other populations. The distribution around the regression (fig. 6) appears, hence, to be trimodal. The two specimens from Ehringsdorf, representing a form stratigraphically and morphologically very close to that from Taubach, fit in with the intermediate mode.

A somewhat similar suggestion of three modes is given by the distribution of *"deningeri"* (figs. 5, 6), and the conditions are so similar to those in *taubachensis* that a fairly close relationship between these two forms (of which *"deningeri"* is the older) appears probable.

A number of cave bear populations have also been considered, but they are not included in my figures, since they do not add anything to the information given in figure 1; all show a single mode of variation around the spelaeid regression (Mixnitz, 40 specimens; Slouper Cave, 16 specimens; Teufelslucken at Eggenburg, 6 specimens; Trosketa Cave, Spain, 6 specimens; various localities, 15 specimens; and from Soergel's data: Hohlestein Cave, 7 specimens; Sirgenstein Cave, 4 specimens; various localities, 6 specimens; all in all, 100 specimens).

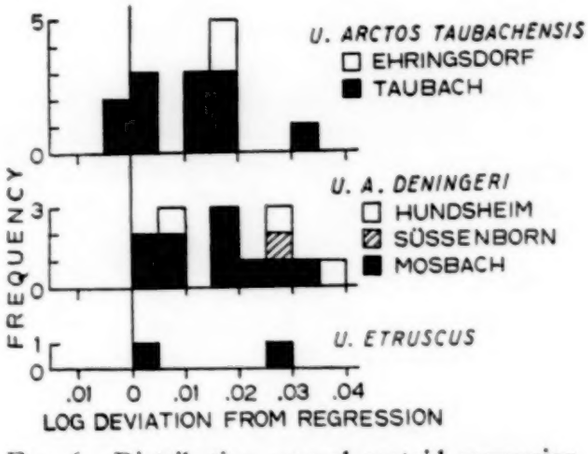

FIG. 6. Distribution around arctoid regression for fossil samples of figure 5, as labelled.

INTERPRETATION

The following is a tentative interpretation of the evidence at hand. I am fully aware that some of it may permit somewhat different conclusions; the possibilities should be evident to any reader with a knowledge of genetics and need not here be enumerated. I have tried to outline a coherent picture as suggested by the data, in accordance with our general information on evolutionary mechanics for the time being. On some essential points the interpretation appears to be considerably fortified by the fact that analogous results have obtained for several other mammal populations (see Kurtén, 1954 a, b), but many conclusions may still be controversial.

The arctoid pattern, which appears to be in evidence from *U. etruscus* on in the arctoid line, may be tentatively homologized through the whole line of descent. Similarly, the spelaeid pattern is in evidence in many populations in both lines from *etruscus* on, and may also be tentatively homologized. The two patterns are here considered allelic, and the data, hence, to give an outline of the history of a genetic locus during the Quaternary.

Both alleles would then be present in *U. "deningeri"* and *U. arctos taubachensis*, but in these populations the presence of a high percentage of intermediates would suggest intermediate phenotype in heterozygotes. The frequencies of the two alleles, which may be designated A_a (arctoid) and A_s (spelaeid), in the gene pool of the Taubach population would then be 16 A_a: 8 A_s, or 67 per cent A_a and 33 per cent A_s.[2]

According to the Hardy-Weinberg law, the distribution of genotypes in such a population would be

$$16^2\ A_aA_a + 2 \times 16 \times 8\ A_aA_s + 8^2\ A_sA_s$$

or 44.45 : 44.45 : 11.1. The frequencies of the phenotypes are, in fact, 41.7 : 50.0

[2] $5\ A_aA_a + 6\ A_aA_s = 16\ A_a + 8\ A_s$.

: 8.3. The coincidence is fairly good for so small a sample.[3]

In the Mosbach sample, the frequencies would be around 4 : 4 : 2, which is also close to the calculated frequencies. The small samples from Hundsheim and Süssenborn appear to show a greater preponderance of the spelaeid allele.

The tentative conclusion is that, in the Taubach population, there was a frequency of A_s in the gene pool on the order of 30–35 per cent, and perhaps a slightly higher frequency in the *"deningeri"* populations.

In the recent Finnish population, 2 out of 40 individuals are spelaeid; they will be regarded as A_s homozygotes. The corresponding frequency of A_s in the gene pool of the population would be on the order of 23 per cent.

The Hardy-Weinberg formula also gives the corresponding frequency of heterozygotes: about 35 per cent. In our sample of 40, these should be represented by no less than 14 specimens, a sample which would greatly influence the shape of the distribution in figure 2. No such intermediates have, however, been observed . It can be shown that this absence has a very high statistical significance, and we may infer that conditions of phenotypic expression are different in the Pleistocene and recent *U. arctos*.

The same conclusion is suggested by the conditions in the recent Pyrenean population, where one specimen out of four is spelaeid, the others being normal arctoids.

The Swedish and Norwegian populations have so far shown no trace of spelaeids.

All populations of *Ursus spelaeus*, finally, appear to have lost the arctoid allele completely. The spelaeid allele, on the other hand, may be tentatively homologized through *"deningeri"* to *etruscus*, and ultimately with that in our recent form.

Finally it must be emphasized that not all differences between the spelaeid and arctoid M^1 (apart from size) can be ascribed to a single mutation. The difference in cusp form, for instance, has been touched upon above; it is also characteristic of M^2 and suggests a morphogenetic effect, such as described by Butler (e.g. 1952). Functionally it may be related to feeding habits.

Discussion

The hypothetical nature of much in the interpretation given above has already been stressed. We shall assume, however, that it is valid in essentials, and proceed to an evaluation of the data and conclusions in terms of general evolutionary principles.

The fixation of different allometry patterns in *U. arctos* and *U. spelaeus* will be regarded as a result of selection, operating on the genetic materials available in the populations. A possible clue to the selective advantage of different allometries in different populations is found if we imagine the allometric pattern of *U. arctos* projected into the larger size of *U. spelaeus* (see also Phleger and Putnam, 1942, p. 559, and Kurtén, 1954 a, b). The result would be a very hypsodont tooth (see fig. 2). In the succeeding tooth, M^2, on the other hand, there is a nearly isometric relation between height and length. The first molar would then jut out of the tooth row and probably inconvenience its bearer. In the von Nordmann collection of cave bears, such patterns do in fact turn up among other molars. There is a monstrous M_2, which is extremely hypsodont, and an almost equally aberrant M_3 of an analogous pattern (in the latter case the effect is less striking to the eye, as the *Ursus* M_3 is normally very brachyodont); both of these deviate strongly from the normal allometry trends of the teeth in question, and may, perhaps, represent random mu-

[3] This is not a circular argument. A distribution, for instance, of 7 : 2 : 3 would also give 16 : 8, being however at variance with the Hardy-Weinberg law.

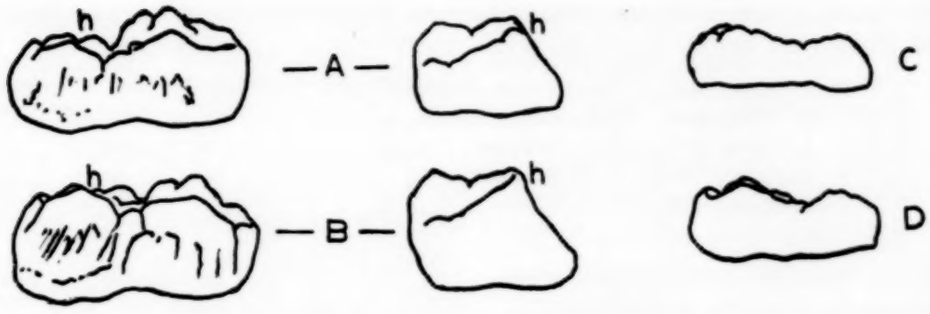

FIG. 7. Normal and aberrant lower molars of *Ursus spelaeus* from Odessa. A-B, M_2, both of same length, A normal, B with hypertrophied hypoconid (h), possibly a mutant (external and posterior views); C-D, M_3, external views, both of same length, C normal, D abnormally hypsodont, possibly a mutant.

tation without selective advantage (fig. 7). Both teeth are of young animals (the M_3 was probably not erupted) and may well have belonged to one individual.

Conversely, the *U. spelaeus* M^1 pattern would of course result in a very brachyodont tooth in a small *U. arctos,* which would wear down sooner than its neighbours; here, again, the disadvantage is readily grasped.

Now it is interesting to note that the spelaeid type is more predominant, the larger the mean size of the tooth in a population.[4] This appears in the surprising constancy of the mean height-length index for the molars in different bear populations despite marked differences in gross size. This index varies around 40 (table 2), and the means, when plotted on a log diagram as in figures 1 and 5, fall approximately on an isometric line. With phyletic growth, thus, the spelaeid type would seem to be encouraged by selection; with phyletic dwarfing, the arctoid.

This would also seem to offer a functional explanation of the supposed intermediate inheritance that has been suggested for the large-sized Pleistocene brown bears. These forms were about intermediate in size between the now-living European *arctos* and the cave bear, and so an intermediate allometry pattern would have been advantageous. This would account for selection in favour of heterozygotes with phenotypically intermediate traits, and may have brought about an evolution in dominance by means of modifiers.[5] Continued selection in favour of heterozygotes would favour the retention of both genes in the gene pool, in certain proportions, depending on the selective value of the three genotypes arising from their combination. The apparent frequencies in *taubachensis* and *"deningeri"* agree with expectation, and we may probably conclude that both forms show a relation that was optimal for a bear of that average size.

The apparent evolution of dominance from the *taubachensis* stage to that of the recent population would seem somewhat inconsequential, since it was accompanied by only a slight reduction of the incidence of A_s (about 33 per cent in *taubachensis,* about 23 in the recent Finnish population). As stated before, I am inclined to believe that *taubachensis* represents a local population that played a minor role in the ancestry of the recent European

[4] In the first place, this appears to some extent to be due to the phenomenon of compensation (see Rensch, 1954). The mutant first molars of the Finnish specimens may have attained their great length simply because less material was needed in building up their height.

[5] Granting that there was a dominant-recessive relation in *etruscus,* as the all too scanty data seem to indicate. The spelaeid allele most probably appeared first in this species, since its ancestors were still smaller (the oldest forms, within the genus *Ursavus,* are on yet another regression, which would be still further to the left in our graphs).

TABLE 2. *Mean hypsodonty indices (100 × paracone height/crown length) in bear populations*

Ursus a. arctos, recent, Finland	43
U. a. taubachensis, Pleistocene, Taubach	41
U. a. "deningeri," Pleistocene, Mosbach	39
U. spelaeus, Pleistocene, Odessa	40
U. spelaeus, Pleistocene, Mixnitz	40
U. spelaeus, Pleistocene, Dachstein	38

bears, as *arctos* appears to have been very rare in Europe during the last glaciation. The most important part in this ancestry must probably be attributed to such populations as that of Ksar Akhil, Lebanon, in which there is no trace of intermediates (the same appears to be true for the Chinese populations from Choukoutien and other Pleistocene sites).

As noted above, the arctoid allele appears to have been completely lost in *spelaeus*. This is especially conspicuous regarding the dwarf form from the Schreiberwand Cave, Dachstein ("hochalpine Kleinformen," Ehrenberg). The presence of arctoids would seem natural in this population, but I have found none, and the M^1 is therefore unusually brachyodont on an average. This is probably to be interpreted as follows: The Dachstein bear descended from normal large-sized cave bears, in which the arctoid allele was already lost, and no back-mutation was incorporated in the gene pool.

The absence of A_s in the Swedish and Norwegian populations—all in all 33 specimens—may be due to sampling chances. It may also reflect actual total fixation of A_a in these semi-isolated populations, which number relatively few heads. The presence of A_s in the Finnish population might actually be due to the fact that this population is continually being reinforced from the east. Through northern Russia there is continuity with the large Siberian forms, among which the retention of A_s may still be favoured by selection.

We have finally to consider the presence of A_s in the completely isolated, small Pyrenean population. As long as little is known of the Middle European populations in historical times, much light cannot be shed on this question; but in such small populations random changes in gene frequency may occur, which might account for the apparently high frequency of A_s.

SIZE TRENDS DURING THE QUATERNARY

Changes in this allometry are thus relegated to the status of by-products of evolution in size. The primary change was phyletic dwarfing or phyletic growth, evolution in allometry following suit. This should not, of course, be construed as a statement that the bears initially grew large (or small) and then started changing allometry in order to become optimally adapted. Intermediate forms such as *taubachensis* or *"denengiri"* indicate a dynamic equilibrium, and such an equilibrium may be postulated to have existed throughout, change in the two characters being roughly simultaneous.

TABLE 3. *Mean lengths of first upper molar in bear populations*

Ursus etruscus, basal Pleistocene, Val d'Arno	21.84±.19
U. e. gombaszögensis, basal Pleistocene, Gombaszög	24.5[a]
U. arctos "deningeri," middle Pleistocene, Mosbach	25.64±.65
U. a. taubachensis, last inertglacial, Taubach	24.24±.26
U. spelaeus, late Pleistocene, Odessa	29.89±.14
U. spelaeus, late Pleistocene, Dachstein	26.63±.26
U. arctos nemoralis, postglacial, Denmark	23.70±.48
U. a. arctos, recent, Fennoscandia	21.12±.14

[a] From Kretzoi.

Unfortunately the changes in size through the 1,000,000-year span of the Quaternary cannot at present be mapped in detail. Table 3 gives the mean lengths of M^1 in a number of bear populations; the data are partly original, partly from Soergel (*op. cit.*) and Degerbøl (1933). For the cave bear line, a relatively simple history is indicated—a steady increase, reversed shortly before extinction; but the stratigraphic position of the Dachstein population is by no means finally settled. As to the brown bears, the late glacial and postglacial data indicate rather irregular temporal and local size trends, and it is a reasonable assumption that similar changes may have occurred during earlier parts of the Pleistocene, possibly in conjunction with the extreme climatic oscillations.

Apparently, size changes may be quite rapid. The decrease from the subfossil *nemoralis* Degerbøl of Denmark to the recent Fennoscandian subspecies, which may be taken to have ocurred during a period on the order of 10,000 years, is almost precisely equivalent to the increase from *etruscus* to *taubachensis*, involving the main part of the Pleistocene. It might of course be argued that the subfossil Danish form is not truly ancestral to the recent Fennoscandian one. This would, however, necessarily imply the complete extinction of the Danish form (and of the almost equally robust subfossil Swedish one), and a subsequent repopulation by another stock; otherwise, the hypothetical small immigrant would have been genetically swamped by the aborigine, which thereby necessarily partook in the ancestry of the recent form. To some extent, however, such gene flow has probably played a part in the shaping of such rapid size trends.

This instance should also, in the opinion of the present writer, be kept in mind when the general trends of phyletic dwarfing in Quaternary mammals (possibly including man) are evaluated; none of them is established on continuous long-range sequences, and the impression of a steady, slow trend may well be spurious.

Conclusions

The arctoid and spelaeid allometries are tentatively interpreted as representing a genetic unit difference. It should be emphasized that this may only be accepted as a working hypothesis, since the evidence in hand so far is not abundant, and the genetic background may be considerably more complicated. This also holds for the interpretation of intermediates within the Pleistocene *Ursus "deningeri"* and *U. arctos taubachensis* populations as heterozygotes with intermediate phenotype.

It is concluded that the arctoid allele, or type of allometry, was wholly lost in the true *U. spelaeus*, whereas the spelaeid one is retained in some recent *U. arctos* populations, though possibly not in all. Both alleles, or types of allometry, are traced back to the lower Pleistocene *U. etruscus*, the common ancestor of *U. spelaeus* and *U. arctos*.

The fairly strong allometry in both forms leads to inadaptive changes in tooth crown shape with excessive change in size. The interplay between two, or more, different types of allometry, in proportions reflecting gene frequencies conditioned by selection, permits forms of different gross size to retain an optimal mode in crown shape.

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VARIABILITY AND EVOLUTIONARY RATE IN THE OREODONTS

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INTRODUCTION

An increasing awareness of the importance of the role of the population as opposed to that of the individual has been one of the major trends of the past several years in evolutionary research. This trend can be discerned in both the botanical and zoological aspects of such disciplines as genetics, ecology, taxonomy, and paleontology. The shift in interest from individual to population has necessitated a renewed study of variation in natural groups since individuals in nature are never phenotypically, and almost never genotypically, identical. The study of variation and its relation to the mechanics of evolutionary change in fossil materials has been hampered in the past by the paucity of species for which an adequate sample was available as well as the reluctance of many paleontological practitioners to stray outside the confines of the typology concept. Happily, continued success in the field has alleviated (at least in part) the first obstacle and an increasing understanding of evolutionary dynamics, the second. Simpson (1944, 1953) has given the most complete expression of recent paleontological thought on problems in which characteristics of populations, including variation, are of prime concern. Most types of variation, to be studied adequately, must be approached not only from the biological point of view but also with the statistical tools of the biometrician.

In the above-mentioned work, Simpson analyzed statistically the relationship between variability and speciation in a phyletic series of Jurassic ammonites. He interpreted the reduction of variation at points of speciation as due to an unequal segregation of variability in the parental population. This point has received practically no attention in studies of vertebrate evolution. It will form one of the main topics of interest in the present paper. The term, variability, will be used throughout as the potentiality or the capacity of organisms to differ from each other as distinguished from its actual realization or expression, variation. In genetic terms variability would represent genotypic differences, variation phenotypic differences. The degree of correlation between the two is obviously very high.

As the gaps in many of the well-known phylogenetic series have become progressively reduced by new field discoveries, paleontologists have concerned themselves not only with readjustments and greater refinements of the phylogenies involved but also with the rates at which such changes took place with an eye to the causal factors involved. Although most fossil lineages are too imperfectly known to lend themselves to such quantitative treatment, the past decade has seen a great increase in the number of vertebrate groups whose evolutionary rates have been studied quantitatively.

The problem of the relationship between variation and rates of change in fossil populations has received little direct study up to the present time. Simpson (1944) made a preliminary analysis of pairs of allied living species, one of which has evolved rapidly, the other at more moderate rates (e.g. horses and tapirs). He found that the more slowly evolving member of each pair showed a variability at least as great as in the allied, more rapidly evolving line and adds "there is

even some evidence, which requires further checking before it can be definitely accepted, that conservative groups are sometimes exceptionally variable." Most authors, while not attacking this problem *per se*, seem to feel that rapidity of change and variability should show a high positive correlation in any given phyletic sequence. It is true that this relationship should hold almost invariably if, by variation, is meant successive intergroup variability. Thus a population, whose mean for a linear measurement is changing more rapidly in time than that of a second population, will have a greater successive intergroup variation in this character—but what of the contemporaneous intragroup variation in the two lineages differing in evolutionary rate? Here the situation seems to be less clear. Would we expect to find greater or less intragroup variability in a lineage which is changing relatively rapidly as opposed to a more conservative line? This is the second major problem to which the present paper is addressed.

Two closely related, abundantly represented lineages, coexisting at the same time and place (thus permitting the use of absolute rates of change) and exhibiting a marked disparity in the rates of changing of several characters, would present an excellent opportunity to obtain information on the relation of contemporaneous intragroup variability to rates of change as well as to speciation. These criteria were satisfied by a study of selected lineages among an extinct group of Tertiary artiodactyls, the oreodonts. In addition to meeting the above-named requisites, this group has recently undergone taxonomic revision by Schultz and Falkenbach (1940, 1941, 1947, 1949, 1950). A large collection accumulated during almost twenty years of field work and housed at the Frick Laboratory, American Museum of Natural History, and at the University of Nebraska State Museum provided the basis for this revision.

The oreodonts are an extremely abundant, exclusively North American, group of pig-like artiodactyls ranging in time from the Late Eocene to the Middle Pliocene. Joseph Leidy, one of the early students of the group, referred to them as "ruminating hogs." The typical oreodonts are represented in the taxonomic hierarchy as the Family Merycoidodontidae. Although the group is among the most abundant of Tertiary mammals (particularly in the Oligocene and Miocene), the ancestry is not definitely known. The progenitors are to be sought among the primitive Eurasian artiodactyls of the Early Eocene but close affinities with a specific group are lacking. The oreodonts would perhaps rival the horses as a textbook example of evolution were it not for the fact that there is no familiar living representative and evolution in the group was considerably more conservative than in the more spectacular equid line.

The results of a comparison of the variability and evolutionary rates of 23 characters in two subfamilies of oreodonts are given below. Measurements were taken on approximately 325 individuals representing 10 different species, 5 in each subfamily. The time is Middle to Late Miocene encompassing approximately 12 million-years and the locale is The Great Plains (with the exception of one California species).

The Fauna and Its Environment

The two subfamilies treated in the present study are the Merycochoerinae and the Merychyinae. They are two of a total of five subfamilies described thus far by Schultz and Falkenbach. All of the specimens measured were in the Frick Laboratory, American Museum of Natural History. The phylogenetic relationships of the contained species of the two subfamilies are shown in Fig. 1. In addition to the species studied, Schultz and Falkenbach (1940, 1947) have distinguished in each of the two subfamilies six additional species, all of which are too poorly

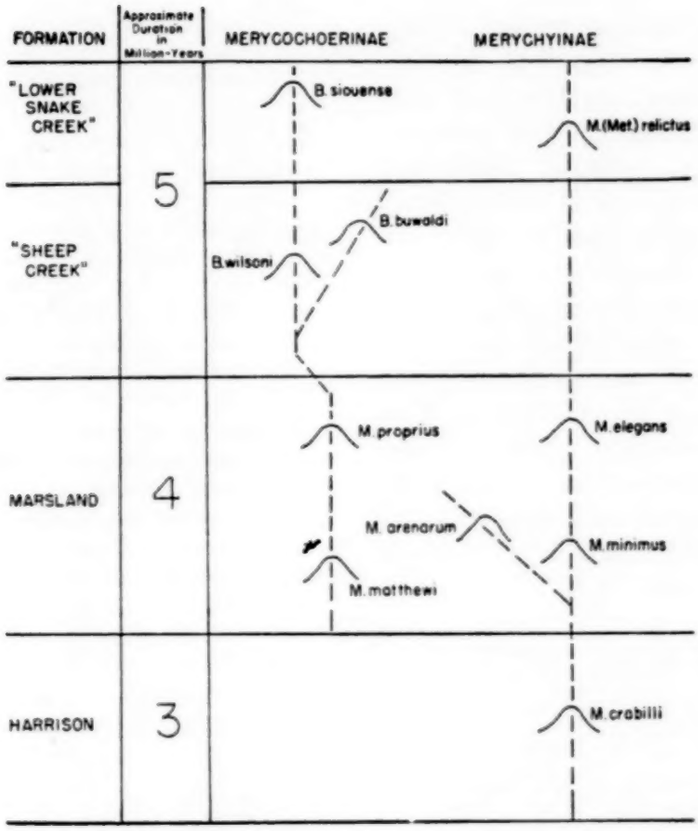
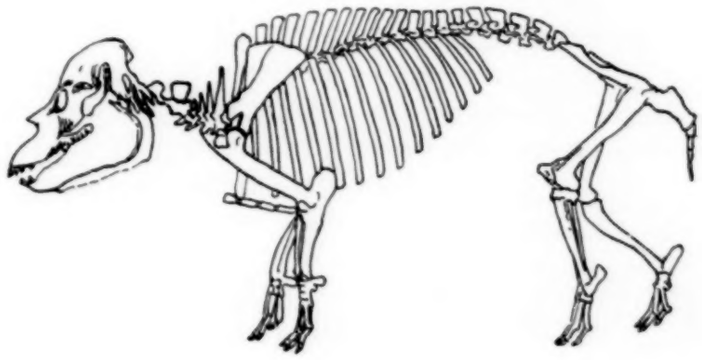


FIG. 1. The phylogenetic and stratigraphic relationships of two subfamilies of oreodonts, the Merycochoerinae and the Merychyinae. The total duration of time in this Middle and Late Miocene sequence is estimated at 12 million-years.

known at the present time to be included in a quantitative project of this nature.

Merycochoerinae. This subfamily is the most "progressive" of the two, evolving at a moderately rapid rate in most of its characters. The forms here represented are short-limbed, heavy creatures with pig-like proportions (fig. 2). The nasals show a progressive retraction from the inception to the termination of the lineage with the probable attendant development of a tapir-like proboscis. Both eyes and ears were placed relatively high on the head. A change from a plains-



Merycochoerus

FIG. 2. A typical representative of the larger, more "progressive" subfamily, the Merycochoerinae.

dwelling to a semi-aquatic habitat is suggested. This is the larger of the two subfamilies, the basal length of the skull averaging about 250 mm. The teeth are selenodont (crescentic-shaped cusps) and brachyodont (low-crowned). The dental series lacks diastemata and the lower canines have been transformed into functional incisors while the P_1 has become caniniform. The robust limbs have four functional digits and remain virtually unchanged throughout the sequence. This subfamily embraces two genera, *Merycochoerus* and *Brachycrus*. A brief description of the genera and their included species follows (modified from Schultz and Falkenbach, 1940, 1947).

Merycochoerus
- Geologic occurrence: Marsland fm.
- Geographic occurrence: Neb., Wyo.
- Diagnostic characters:
  - Nasals robust and becoming retracted
  - Infraorbital foramina above region of M^1
  - Dentition brachyodont
  - Limbs comparatively robust
  - Larger in almost all measurements than *Brachycrus*

M. matthewi (11 skulls)
- Geologic occurrence: Lower part of Marsland fm.
- Geographic occurrence: [1] Neb., Wyo.
- Diagnostic characters:
  - Smaller and lighter skull (and mandible) than *M. proprius*
  - Nasals only slightly retracted
  - Muzzle region of skull much lower than in *M. proprius*
  - Lighter limbs but about same length as *M. proprius*

M. proprius (24 skulls, 20 mandibles)
- Geologic occurrence: Upper part of Marsland fm.—never found in association with *M. matthewi*.
- Geographic occurrence: Neb.
- Diagnostic characters:
  - Skull and mandible larger and more massive
  - Nasals more retracted than *M. matthewi*
  - Limbs heavier than *M. matthewi*

Brachycrus
- Geologic occurrence: Sheep Creek fm.
- Geographic occurrence: Neb., Calif.
- Diagnostic characters:
  - Nasals light and greatly retracted
  - Infraorbital foramina above region of M^2
  - Dentition moderately hypsodont
  - Limbs comparatively light
  - Smaller in almost all measurements than *Merycochoerus*

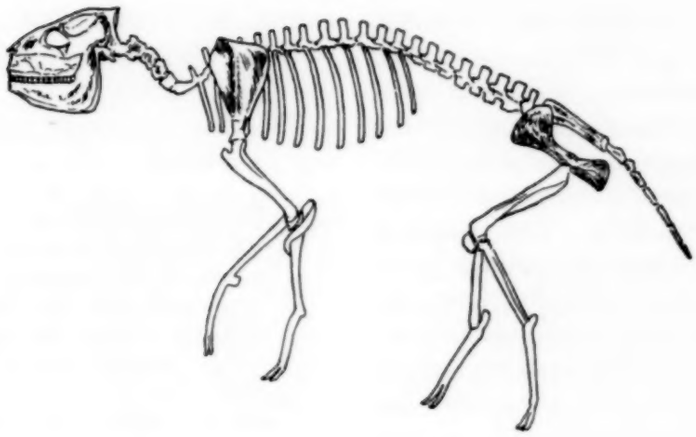
B. wilsoni (19 skulls, 22 mandibles)
- Geologic occurrence: Sheep Creek fm.
- Geographic occurrence: Neb.
- Diagnostic characters:
  - This species is larger than either of the other two species of *Brachycrus* in almost all of the measurements which were considered. Most of the measurements obtained in any quantity were on the dentition.

B. buwaldi (19 skulls)
- Geologic occurrence: Barstow, Calif. (Sheep Creek equivalent)
- Geographic occurrence: Calif.
- Diagnostic characters:
  - Smaller than *B. wilsoni* but larger than *B. siouense* in nearly all measurements which were by necessity limited almost entirely to the dentition as in *B. wilsoni*.

B. siouense (46 skulls, 31 mandibles)
- Geologic occurrence: "Lower Snake Creek," i.e., upper part of Sheep Creek fm.
- Geographic occurrence: Neb.
- Diagnostic characters:
  - Smallest of *Brachycrus* species here considered
  - Best represented of the *Brachycrus* species

Merychyinae. Almost all of the characters studied in this subfamily change at a slower rate than comparable features in the Merycochoerinae. Nothing as striking as the nasal retraction in the larger subfamily takes place in this series. The group is characterized by a short, bullet-like head and relatively slender limbs and feet (fig. 3). It is considered smaller than the Merycochoerinae, averaging about 150 mm. in basal skull length. The dentition is similar to that of the Merycochoerinae except for the expected differences in size. The limbs remain conservative except for a slight reduction in the second and fifth metapodials in the later representatives of the line. The most prominent feature of their evolution seems to be a slow but steady increase in size with a consequent better general adaptation of a cursorial form to a plains

[1] Type specimen is from S. Dak. but was not available for this study.



Merychyus

FIG. 3. A typical representative of the smaller, more conservative subfamily, the Merychyinae.

environment. This subfamily is represented by the genera *Merychyus, Paramerychyus,* and *Oreodontoides*; however, only the first-named has been included in the study. The latter two are very poorly represented in the collections and appear to be somewhat aberrant off-shoots from the main phylogenetic line represented by the various species of *Merychyus.* Diagnostic characteristics of the species are based largely on size relationships. A description of the species included in the genus follows:

M. crabilli (18 skulls)
Geologic occurrence: Harrison fm.
Geographic occurrence: Neb., Wyo.
Diagnostic characters:
Smallest in genus, smaller than *M. minimus,* its descendant.

M. minimus (52 skulls, 33 mandibles)
Geologic occurrence: Lower part of Marsland fm.
Geographic occurrence: Neb., Wyo., S. Dak.
Diagnostic characters:
Larger than *M. crabilli,* smaller than either *M. arenarum* or *M. elegans.* There is some overlap with *M. arenarum* (both morphologically and stratigraphically); the two are best separated by limb size, the limbs of *M. minimus* being shorter and lighter.

M. arenarum (60 skulls, 29 mandibles)
Geologic occurrence: Upper part of lower Harrison fm.
Geographic occurrence: Neb., Wyo.
Diagnostic characters:
Considerably larger than *M. minimus*
Malar deeper than that of *M. minimus*
Limbs longer and more massive than in *M. minimus*

M. elegans (20 skulls, 33 mandibles)
Geologic occurrence: Upper part of Marsland fm.
Geographic occurrence: Neb., Col.
Diagnostic characters:
Type of genus is very similar in size to *M. (Met.) relictus*

M. (Metoreodon) relictus (26 skulls, 46 mandibles)
Geologic occurrence: "Sheep Creek" and "Lower Snake Creek"—Sheep Creek fm.
Geographic occurrence: Neb.
Diagnostic characters:
Separable from *Merychyus* because of complicated superior and inferior premolars of *M. (Metoreodon)* Skull, mandible, and limbs are approximately the size of *M. elegans*

The stratigraphy. The chronological relationships of the strata concerned in this sequence are given in figure 1. The total thickness of the section is about 700 feet. The "Lower Snake Creek" and "Sheep Creek" are considered to be the upper and lower parts of the Sheep Creek formation respectively, following Lugn (1939). The Sheep Creek and Marsland formations are part of the Hemingford group; the Harrison formation is included in the Arikaree group. The west-central Great Plains equivalent of the

Barstow formation of California (*Brachycrus buwaldi*) is considered to be the Sheep Creek formation. Sand, silt, and clay are the predominant lithological features of the stratigraphic section, representing primarily flood plain deposits with interspersed channel fills. The channels become more frequent in the younger portion of the sequence with finds in the Sheep Creek formation being almost entirely of this type. Although the sharp morphological differentiation between the two subfamilies almost certainly insures some ecological differences (semi-aquatic as opposed to cursorial, plains-dwelling), field collecting has unfortunately failed to establish a correlation between either of the groups and a particular paleoecological niche as reflected in the field occurrences. This correlation, however, would be expected to be lacking in the Sheep Creek where most all of the finds (in both subfamilies) are in channels associated with horses, deer, and camels among others.

The climate on The Great Plains during this time span was more equable and less subject to extremes than in the same area today. The general trend of the Middle and Late Tertiary of a cooler, drier clime was in evidence by Miocene times.

All the species occur in The Great Plains area except *Brachycrus buwaldi* which has been found only in the Barstow formation of southern California. Other species in these subfamilies (not included because of the lack of an adequate sample) have been described from Montana, New Mexico, and Idaho.

The Measurements

Seventeen measurements were made on the skulls and six measurements on the mandibles of approximately 325 specimens in the 10 species. Of the 23 measurements 10 were on the dental series or of individual teeth. Distortion and imperfect preservation have in each species reduced the total number of measurements below the total number of specimens. This is particularly true in the Merycochoerinae.

The measurements and their symbols are as follows:

(1) Basal Length (Bas_L)—The distance from the posterior base of I^1 to the anterior notch of the foramen magnum

(2) Zygomatic Width (Zy_W)—The greatest distance across the zygomatic arches on a line normal to the axial plane of the skull

(3) Facial Length (Fac_L)—The distance from the anterior base of the canine to the anterior rim of the orbit

(4) Palatal Width at the M^3 ($Pal_M{}^3$)—The distance between the anterior lobes of the M^3 on a line normal to the axial plane of the skull

(5) Palatal Width at the Canines (Pal_c)—The distance between the medial edges of the canines on a line normal to the axial plane of the skull

(6) Muzzle Width (Muz_W)—The width of the muzzle at the P^1 on a line normal to the axial plane of the skull

(7) Length of the Superior Premolars ($Spre_L$)—The length of the superior premolar series measured at the base

(8) Length of the Superior Molars ($SMol_L$)—The length of the superior molar series measured at the base

(9) Length of the M^3 (M^3)—The length of the M^3 measured at the external edge at the base

(10) Width of the M^3 ($M^3{}_W$)—The width of the anterior lobe of the M^3 measured at the base

(11) Length of the P^4 ($P^4{}_L$)—The length of the P^4 measured at the external edge of the crown

(12) Width of the P^4 ($P^4{}_W$)—The greatest width of the P^4 measured at the base along a line normal to the axial plane of the skull

(13) Occipital Condyle Width (Occ_W)—The greatest width across the occipital condyles on a line normal to the axial plane of the skull

(14) Interorbital Width (Io_W)—The minimum distance between the inner margins of the orbits normal to the axial plane of the skull

(15) Orbital Length (Orb_L)—The greatest length of the orbit along a line parallel to the axial plane of the skull

(16) Malar Depth (Mal_D)—The minimum depth of the malar below the orbit on a line normal to the axial plane of the skull

(17) Length from the Infraorbital Foramen to the M^3 (F_{IO})—The distance from the anterior edge of the infraorbital foramen to a line drawn perpendicularly from the anterior edge of the M^3 along a line parallel to the axial plane of the skull

(18) Length of the Mandible ($Mand_L$)—The greatest distance between the anterior edge of the P_1 at the base and the posterior edge of the ramus along a line parallel to the long axis of the mandible

(19) Height of the Mandible ($Mand_H$)—The distance between the anterior edge of the P_2 at the base and posterior border of the symphysis along a line normal to the long axis of the mandible

(20) Length of the Inferior Premolars ($IPre_L$)—The length of the inferior premolar series measured at the base

(21) Length of the Inferior Molars ($IMol_L$)—The length of the inferior molar series measured at the base

(22) Length of the M_2 (M_{2L})—The length of the M_2 measured along the external edge at the base

(23) Width of the M_2 (M_{2W})—The width of the anterior lobe of the M_2 measured at the base

The mean ($\bar{x}$) and the standard deviation (s) were calculated for each measurement in each species. From these parameters a relative measure of dispersion, the Pearsonian coefficient of variation (V), was obtained using the formula $100s/\bar{x}$. A valid comparison of the relative variation of homologous continuous variates can be made by the use of V only where the group in question has a definitive adult state, e.g., the teeth and skeletal parts of mammals. Values of V obtained from groups which exhibit indeterminable terminal growth (e.g., most amphibians and reptiles) do not express variability in its true biological sense (Olson, 1951). Only adults (i.e., forms in which the third molar is completely erupted) were used in the present study. A standard error can be calculated for the coefficient of variation ($V/\sqrt{2N}$) and thus a standard error of the difference (σ_d) between sample V's can be obtained as follows (Croxten and Cowden, 1939):

$$\sigma_d = \sqrt{\sigma^2_{V_1} + \sigma^2_{V_2}}$$

The *t* test of significance of difference between sample V's can then be made by comparison of the actual difference (σ_d) with the standard error of the difference (σ_d) as in the well-known case of comparison of sample means.

Rates of evolution are commonly given in either morphological or taxonomic terms and may be expressed in relation to absolute time, a factor correlated with absolute time (such as thickness of the strata), or by changes in other structures or populations (Simpson, 1953). Morphological rates of unit characters expressed in terms of a temporal (absolute time) scale seemed most appropriate for this study. The formula used was proposed by Haldane (1949), i.e.,

$$\frac{\log_e x_2 - \log_e x_1}{t},$$

in which x_1 and x_2 are, respectively, the population means at the beginning and end of the temporal sequence and t is the interval of time expressed in terms of absolute years. The resultant figure is the mean percentage increase per annum. This may be converted to rate per million-years by multiplying by 1 million-years. For example the figure 5.0×10^{-8} indicates a mean increase of 5% per million-years. The value is negative if the size of the structure is decreasing.

The number of million-years assigned to each formation (based on a total of 16 million-years in the Miocene) is, of course, only an approximation (fig. 1). However, the use of an absolute time scale is justifiable since both lineages are found in the same stratigraphic sequence (with the exception of the oldest species in the Merychyinae which has no contemporary in the Merycochoerinae). Thus a comparison of rates in the two lines is relatively independent of the absolute scale chosen and enables comparisons to be made with other lineages at various times and places.

The results obtained from the computation of the coefficients of variation and the

TABLE 1. *The coefficients of variation (V) and the mean ($\bar{X}$) for 23 characters in 10 species of oreodonts in the Merycochoerinae and Merychyinae*

Species \ Character		BasL	Zy_W	FacL	Pal_{M1}	Pal_6	Muz_W	SPreL	SMolL
	N	16	15	18	30	30	30	21	32
	$\bar{x}$	231.81±2.50	172.93±2.89	126.28±1.94	43.80± .63	23.83± .37	54.60± .62	50.05± .53	72.38± .48
B. siouense	V	4.31± .76	6.47±1.18	6.53±1.09	7.92±1.02	8.60±1.11	6.47± .84	4.84± .75	3.87± .47
	N				8		5	8	18
	$\bar{x}$	—	—	—	50.88±1.60	—	58.00±1.00	53.50±1.26	75.06± .73
B. buwaldi	V				8.88±2.22		3.86±1.11	6.64±1.66	4.13± .69
	N							8	12
	$\bar{x}$	—	—	—	—	—	—	56.25± .80	79.33±1.01
B. wilsoni	V							4.00±1.00	4.42± .90
	N	7	8	8	6	5	6	9	72
	$\bar{x}$	277.57±2.80	222.00±5.05	154.50±2.60	55.17±2.08	41.80±1.11	72.33±2.16	61.00±1.14	88.00±1.27
M. proprius	V	2.67± .71	6.43±1.18	4.76±1.19	9.23±2.66	5.96±1.88	7.12±2.06	5.62±1.32	4.99±1.02
	N	7		9	5		7	9	9
	$\bar{x}$	272.43±3.59	—	141.00±3.15	55.80±1.17	—	71.14±2.00	62.00± .76	85.22±1.02
M. matthewi	V	3.49± .93		6.71±1.58	5.13±1.48		7.45±1.99	3.69± .87	3.60± .85
	N	6	6	7	6	6	8	12	19
	$\bar{x}$	150.67±1.95	101.33±3.19	65.14±1.00	31.33±1.46	15.85± .89	32.63± .89	33.08± .25	42.74± .12
M. (Met.) relictus	V	3.17± .92	7.71±2.23	4.07±1.09	11.43±3.30	13.82±3.99	7.72±1.93	2.63± .54	4.23± .69
	N	10	8	11	12	12	12	18	18
	$\bar{x}$	154.80±2.76	106.50±1.89	67.18±1.12	30.58± .88	16.14± .35	34.00± .72	33.22± .42	42.56± .56
M. elegans	V	5.64±1.26	5.02±1.26	5.55±1.18	9.97±2.04	7.43±1.52	7.62±1.49	5.36± .89	5.55± .93
	N	33	25	35	22	27	30	39	40
	$\bar{x}$	156.97±1.53	107.56±1.65	70.71± .86	29.05± .69	16.26± .26	33.40± .39	34.10± .34	44.78± .36
M. arenarum	V	5.58± .69	7.67±1.08	7.16± .86	11.19±1.69	8.36±1.14	6.32± .82	6.25± .71	5.14± .57
	N	30	23	40	26	25	29	34	38
	$\bar{x}$	133.70±1.54	90.96±1.60	58.43± .79	24.92± .53	14.57± .30	29.00± .42	30.47± .25	39.16± .37
M. minimus	V	6.31± .81	8.43±1.24	8.51± .95	10.83±1.50	10.23±1.45	7.86±1.03	4.82± .58	5.82± .67
	N	7		8	7	7	8	10	14
	$\bar{x}$	127.43±1.89	—	53.75±1.03	25.71±1.31	12.53± .31	27.63± .61	30.00± .61	36.36± .59
M. crabilli	V	3.93±1.05		5.43±1.36	13.50±3.61	7.02±1.76	6.23±1.56	6.47±1.37	6.11±1.15

TABLE I.—*Continued*

Species \ Character		M^3_L	M^3_W	P^4_L	P^4_W	Occ_W	Io_W	Orb_L	Mal_D
	N	34	27	31	33	17	13	13	16
	$\bar{x}$	34.21± .37	24.41± .34	12.77± .11	15.88± .13	50.35±1.01	79.23±2.04	33.46± .34	40.00± .97
B. siouense	V	6.23± .76	7.29± .99	4.78± .61	4.66± .57	8.26±1.42	9.30±1.82	3.65± .72	9.73±1.72
	N	18	7	12	14				
	$\bar{x}$	34.39± .42	25.14± .52	12.86± .18	16.99± .25	—	—	—	—
B. buwaldi	V	5.15± .86	5.45±1.46	4.82±1.39	5.53±1.04				
	N	13	9	18	18				
	$\bar{x}$	37.08± .66	27.22± .44	13.42± .18	17.78± .19	—	—	—	—
B. wilsoni	V	6.39±1.25	4.89±1.15	5.74± .96	4.44± .74				
	N	11	13	16	19	11	7	9	9
	$\bar{x}$	41.64± .65	29.62± .29	14.36± .16	18.26± .25	57.00±1.48	89.86±3.41	35.67±1.03	54.56±1.22
M. proprius	V	5.21±1.11	3.54± .69	4.38± .77	5.91± .96	8.60±1.83	10.05±2.69	8.69±2.05	6.73±1.59
	N	11	6	9	8	7		7	
	$\bar{x}$	39.73± .77	29.50± .43	14.49± .16	19.25± .42	55.86± .95	—	18.14± .87	—
M. matthewi	V	6.42±1.37	3.56±1.03	3.31± .78	6.13±1.53	4.49±1.20		6.03±1.61	
	N	20	19	19	20			7	8
	$\bar{x}$	20.35± .19	13.76± .22	8.21± .76	10.16± .78	—	—	16.29± .50	15.94± .80
M. (Met.) relictus	V	4.23± .67	7.12±1.16	4.02± .65	3.44± .54			5.06±1.35	14.12±3.53
	N	16	14	16	18	5	8	6	9
	$\bar{x}$	19.59± .29	14.19± .32	8.18± .85	10.20± .19	33.20± .92	49.38± .60	26.33± .51	16.79± .68
M. elegans	V	5.97±1.06	8.39±1.59	4.28± .73	7.84±1.31	6.17±1.95	3.42± .86	4.75±1.37	13.40±2.86
	N	46	32	33	39	27	25	22	36
	$\bar{x}$	20.78± .20	15.21± .17	8.68± .09	11.21± .09	34.11± .41	47.40± .88	23.40± .33	17.63± .29
M. arenarum	V	6.54± .68	6.31± .79	6.22± .77	5.26± .60	6.30± .86	9.30±1.32	6.62±1.00	9.70±1.14
	N	38	37	25	34	21	27	25	32
	$\bar{x}$	18.15± .20	13.37± .14	7.77± .11	10.26± .12	28.19± .49	42.41± .80	26.60± .39	14.84± .26
M. minimus	V	6.72± .77	6.43± .75	6.82± .96	6.82± .83	7.98±1.23	9.93±1.35	6.97± .99	10.04±1.17
	N	15	16	13	14	9	8	9	9
	$\bar{x}$	17.03± .28	12.36± .13	7.55± .13	9.79± .11	6.67± .66	39.75±1.35	24.44± .43	13.42± .42
M. crabilli	V	6.28±1.15	6.15±1.09	6.09±1.19	4.39± .83	7.39±1.74	9.57±2.40	5.24±1.23	9.39±2.21

TABLE 1.—*Continued*

Species \ Character		F1O	MandL	MandH	I PreL	I molL	M1L	M1W
	N	29	23	29	20	26	24	23
	$\bar{x}$	52.21± .81	202.70±1.50	47.94± .64	49.85± .47	76.77± .63	21.42± .27	15.60± .17
B. siouense	V	8.33±1.09	3.55± .52	7.15± .94	4.23± .67	4.21± .58	6.21± .90	5.19± .77
	N							
	$\bar{x}$	—	—	—	—	—	—	—
B. buwaldi	V							
	N	5		14	16	13	17	19
	$\bar{x}$	57.60±2.50	—	51.93± .93	54.69± .64	86.92±1.05	24.53± .33	17.36± .19
B. wilsoni	V	9.70±3.07		6.68±1.26	4.64± .82	4.36± .86	5.63± .97	4.86± .79
	N	6	12	9	9	10	14	10
	$\bar{x}$	55.50±2.43	230.17±5.62	53.00±1.87	59.33±1.30	92.70±1.02	25.57± .35	17.99± .26
M. proprius	V	10.74±2.10	8.46±1.73	10.58±2.49	6.57±1.55	3.48± .78	5.08± .96	4.56±1.02
	N	6						
	$\bar{x}$	44.50±2.89	—	—	—	—	—	—
M. matthewi	V	15.89±4.59						
	N	9	16	28	33	36	28	38
	$\bar{x}$	12.72± .68	130.00±2.17	24.86± .35	31.82± .33	48.53± .44	13.71± .20	9.97± .08
M. (Met.) relictus	V	15.96±3.76	6.66±1.18	7.44± .99	5.88± .72	5.38± .63	7.88±1.05	4.81± .55
	N	14	12	24	25	28	28	29
	$\bar{x}$	13.06± .42	131.00±1.77	23.98± .35	32.72± .38	46.75± .45	13.09± .15	9.76± .12
M. elegans	V	12.02±2.27	4.48± .96	7.21±1.04	5.78± .82	5.07± .68	6.19± .83	6.86± .90
	N	20	26	25	25	26	24	23
	$\bar{x}$	13.83± .51	132.23±1.74	22.64± .44	33.84± .52	48.88± .47	13.63± .20	10.08± .14
M. arenarum	V	16.41±2.59	6.72± .93	9.81±1.39	7.62±1.08	4.93± .68	7.34±1.06	6.55± .97
	N	27	27	26	31	30	24	26
	$\bar{x}$	11.16± .38	116.00±1.56	19.72± .35	29.94± .40	42.90± .46	12.23± .16	9.15± .11
M. minimus	V	17.47±2.38	6.97± .95	8.98±1.25	7.41± .94	5.87± .76	6.30± .91	5.90± .82
	N	8						
	$\bar{x}$	10.93± .51	—	—	—	—	—	—
M. crabilli	V	13.17±3.29						

rates of change for the 23 characters in the two subfamilies are given in table 1.

Variability and Speciation

Rosa (1899) proposed what has become known as the "law" of the progressive reduction of variability. According to this concept, depletion of variability should be concomitant with long-range evolution due primarily to the segregation of ancestral variants through speciation. Evolutionary change should then cease when a large number of homozygous populations had finally become established. In table 2 are given the mean values of V for the characters considered in each of the species of oreodonts studied. It can be seen that there is no discernible secular reduction in variation in either subfamily over the 12 million-year span. This supports findings from most other evolutionary sequences in which this factor has been analyzed that in long-range phyletic evolution there appears to be only minor fluctuations in contemporaneous intragroup variation. Any reduction of variability through isolation of a part of a parental population by speciation is evidently soon restored by mutation with selection probably acting as the chief integrating factor.

A concrete example in which the above interpretation seems highly probable is found in the subfamily Merychyinae involving chiefly *M. minimus, M. arenarum,* and *M. elegans* (fig. 1). *M. minimus* is found throughout the lower Marsland formation, *M. arenarum* in the upper part of the lower Marsland, and *M. elegans* in the upper part of the Marsland. Within the Marsland formation of The Great Plains area of western Nebraska and eastern Wyoming the oldest group, *M. minimus,* gives rise to *M. arenarum* by cleavage and soon thereafter (in upper Marsland times) the *M. minimus* population has been sufficiently altered through phyletic transformation to be recognized as a different species, *M. elegans. M. elegans* gives rise to *M. (Met.) relictus* in the overlying Sheep Creek formation. There are no known descendants of *M. arenarum.*

The splitting off of the *arenarum* population should have reduced the variability in the *minimus* group, which might be reflected in its direct descendant *M. elegans.* In table 3 a detailed comparison of the variation in 27 characters in the three species is made (length of the palate (Pal_L) and three ratios of dental characters were added to the previously mentioned 23). *M. minimus* has a mean V of 7.74 for the 27 characters, *M. arenarum* a mean V of 7.17, and *M. elegans* 6.53. *M. minimus* has a greater variation than *M. arenarum* in 20 of the 27 characters and has a higher V in 21 of the 27 when compared with *M. elegans.* In only three characteristics is *M. minimus* lower than both the other two species. However, when the V's for each homologous characteristics are compared, *M. minimus* is statistically significantly greater in only a

Table 2. *The mean V of the characters measured in each species in the two subfamilies.* The number of characters considered in each species is indicated by N. There is no overlap in the range of V's in the two subfamilies, the smallest mean V in the Merychyinae being greater than the largest in the Merycochoerinae.

Subfamily Merycochoerinae	N	Mean V	Subfamily Merychyinae	N	Mean V
Brachycrus siouense	23	6.15	*Merychyus (Met.) relictus*	21	6.83
Brachycrus buwaldi	8	5.56	*Merychyus elegans*	23	6.62
Brachycrus wilsoni	12	5.48	*Merychyus arenarum*	23	7.43
Merycochoerus proprius	23	6.49	*Merychyus minimus*	23	7.89
Merycochoerus matthewi	13	5.84	*Merychyus crabilli*	22	7.12
Grand Mean		5.90	Grand Mean		7.18

TABLE 3. *A comparison of values of V in* M. minimus *with those of* M. arenarum *and* M. elegans. Plus signs indicate the *minimus* value is higher. (See text.)

Character	*minimus*	*arenarum*	sign	difference	*elegans*	sign	difference
Bas_L	6.31	5.58	+	0.73	5.64	+	0.67
Pal_L	6.48	4.99	+	1.49	4.60	+	1.88
Zy_W	8.43	7.63	+	0.76	5.02	+	3.41
Fac_L	8.51	7.16	+	1.35	5.55	+	2.96
Pal_{M^3}	10.83	11.19	−	0.36	9.97	+	0.86
Pal_C	10.23	8.36	+	1.87	7.43	+	2.80
Muz_W	7.86	6.32	+	1.54	7.62	+	0.24
$SPre_L$	4.82	6.25	−	1.43	5.36	−	0.54
$SMol_L$	5.82	5.14	+	0.68	5.55	+	0.27
$M^3{}_L$	6.72	6.54	+	0.18	5.97	+	0.75
$M^3{}_W$	6.43	6.31	+	0.12	8.39	−	1.96
$P^4{}_L$	6.82	6.22	+	0.60	4.28	+	2.54
$P^4{}_W$	6.82	5.26	+	1.56	7.84	−	1.02
Occ_W	7.98	6.30	+	1.68	6.17	+	1.81
Io_W	9.93	9.30	+	0.63	3.42	+	6.51
O_L	6.97	6.62	+	0.35	4.75	+	2.22
M_D	10.04	9.70	+	0.34	13.40	−	3.36
F_{IO}	17.47	16.41	+	1.06	12.02	+	5.45
$Mand_L$	6.97	6.72	+	0.25	4.48	+	2.49
$Mand_H$	8.98	9.81	−	0.83	7.21	+	1.77
$IPre_L$	7.41	7.62	−	0.21	5.78	+	1.63
$IMol_L$	5.87	4.93	+	0.94	5.07	+	0.80
M_2L	6.30	7.34	−	1.04	6.19	+	0.11
M_2W	5.90	6.55	−	0.65	6.86	−	0.96
$\frac{SPre_L}{SMol_L}$	6.54	4.62	+	1.92	4.49	+	2.05
$\frac{M^3{}_W}{M^3{}_L}$	4.87	5.15	−	0.28	7.88	−	3.01
$\frac{P^4{}_L}{P^4{}_W}$	7.74	5.40	+	2.34	5.46	+	2.28
$\overline{X}$	7.74	7.17	+	0.577	6.53	+	1.209

very few. A situation is thus presented in which the magnitude of a given trait (i.e., variation) in one group is greater than that of homologous traits in two other groups in the overwhelming majority of cases (41 out of 54) but is significantly greater in only a very few of these individual cases. In such situations the sign test may appropriately be used to determine whether the preponderance of the higher V's in *minimus* departs significantly from a random distribution.

First of all, a "t" test must be run to determine whether the magnitude of the differences between the homologous V's differ significantly from zero. In the comparison of *minimus* and *arenarum* (table 3) the mean difference in homologous V's was 0.577 which differs significantly from zero at the .03 level of confidence ($t = 2.22$). In the *minimus-elegans* comparison, the mean difference was 1.209 which differs significantly from zero at the .05 level of confidence ($t = 1.99$).

The sign test is a simple nonparametric statistical procedure (i.e., the comparison is between distributions and not between parameters) and is, in general, applicable when the following conditions pertain (Dixon and Massey, 1951):

(a) There are pairs of observations to be compared.
(b) Each of the two observations of a given pair was made under similar conditions (or on homologous structures).

(c) The different pairs were observed under different conditions (or made on non-homologous structures).

A plus sign preceding the difference between each pair of V's signifies that the variation in *minimus* was higher than *arenarum* or *elegans;* a minus sign indicates the *minimus* variation was lower. The symbol r will be used to designate the number of times the less frequent sign occurs. The null hypothesis here is that each difference has a probability distribution with median equal to zero. The null hypothesis shall be rejected when the number of positive and negative signs differ significantly from equality. The relationship between N, r and various levels of confidence (P) are provided in tables (*e.g.*, Dixon and Massey, 1951, table 10). Thus for $N = 27$ and $r = 7$ (the *minimus-arenarum* comparison) there is significance at the .05 level and for $N = 27$ and $r = 6$ (the *minimus-elegans* comparison), there is significance at the .01 level. *M. minimus* is thus shown to have a significantly higher variation than either of the two descendant groups.

The large *minimus* population exhibited a high variability (the highest of any of the ten species measured) and probably was composed of a few partially isolated groups of subspecific scope, although these have not been described as such. One such group was the incipient species, *M. arenarum*. With the complete isolation of *arenarum* there was an actual loss of variability in the parent stock as reflected in the reduced variation exhibited by *M. elegans*. In this fashion part of the original intragroup variability becomes shifted to the intergroup level. This depleted variability has been partially restored in *M. (Met.) relictus*, the descendant of *M. elegans* (table 2).

The study of the variabilities in the three species lends support to the thesis that *minimus* represented the largest, geographically most widespread group, that the *arenarum* population was some-

TABLE 4. *A comparison of the evolutionary rate and coefficient of variation in the Merycochoerinae (1) and Merychyinae (2).* The t value refers to the significance of the difference between V's in the two subfamilies.

	BasL	Zyw	FacL	Pal^3M	Palc	Muzw	Occw	Iow
Rate 1	−1.79	−3.57	−1.23	−2.69	−8.03	−2.95	−1.15	−1.80
Rate 2	+1.40	+1.20	+1.60	+1.65	+1.96	+1.39	+3.13	+3.10
V_1	3.49	6.45	6.00	7.79	7.28	6.23	7.12	9.68
V_2	4.93	7.21	6.14	11.38	9.37	7.15	6.96	8.06
t	2.45	1.00	1.00	2.92	1.83	1.00	1.00	1.00

	OL	MD	F1O	MandL	MandH	SPreL	SMolL	M^3L
Rate 1	−1.46	−4.43	+1.78	−1.82	−1.42	−2.38	−1.81	−1.66
Rate 2	+0.61	+1.44	+1.26	+1.27	+2.58	+0.81	+1.35	+1.48
V_1	6.12	8.23	11.17	6.01	8.14	4.96	4.20	5.88
V_2	5.73	11.33	15.01	6.21	8.36	5.11	5.37	5.95
t	1.00	2.17	2.30	1.00	1.00	1.00	2.45	1.00

	M^3W	P^4L	P^4W	IPreL	IMolL	M_2L	M_2W
Rate 1	−2.11	−1.40	−2.14	−2.49	−2.69	−2.53	−2.04
Rate 2	+0.90	+0.70	+0.30	+0.68	+1.37	+1.27	+0.95
V_1	4.95	4.61	5.33	5.15	4.02	5.64	4.87
V_2	6.88	5.49	5.55	6.67	5.31	6.93	6.03
t	3.06	1.00	1.00	2.17	2.43	1.79	1.87

what smaller, and that *elegans* was the smallest and most homogeneous group. It is interesting to note that in the Frick collections (which represent almost 2 decades of work in this area) *M. minimus* is represented by about 400 specimens, *M. arenarum* by 200 specimens, and *M. elegans* by 160. While not conclusive in and of themselves, these figures also add corroborative evidence to the above-stated hypothesis.

Interspecific and Intraspecific Differences in Variability

The mean V for each species is given in table 2. It can be seen that there is no overlap in the mean figure for each species when the subfamilies are compared, the species of the Merychyinae consistently having the higher value. The mean value of V for each character in each subfamily was obtained by averaging the V's of each of the contributing species in the subfamily (table 4). The Merychyinae also have a higher value of V in 20 of the 23 characters considered. In only 8 of these 20 is the difference between subfamilies significant at the .05 level of confidence. The greater variations of the Merycochoerinae in 3 measurements all lack statistical significance. Since so few significant differences were obtained in comparisons of the variation in each homologous measurement between subfamilies, and, since the preponderance of higher V's in the Merychyinae appears to be meaningful, a comparison of the groups by use of the sign test (see above) seemed appropriate. The mean difference between the V's in the two subfamilies was obtained by adding algebraically the differences between the homologous V's and dividing by the total number (23). This mean difference (1.03) is found to be significantly greater than zero at the $< .01$ level of confidence, demonstrating that, when considered as a unit, the variation in the 23 characters in the subfamily Merychyinae is significantly greater than the variation in homologous measurements in the Merycochoerinae. For the sign test, $N = 23$, $r = 3$, the appropriate tables indicate that the plus and minus signs depart significantly from equality at the $< .01$ level of confidence. Thus not only the magnitude of the difference but the greater frequency of the higher V's in the Merychyinae prove to be significant.

Ninety per cent of the values of V lie between 3 and 10, 95% between 2.5 and 12. This is the usual range for linear measurements of the preservable hard parts of mammals. There appear to be rather definite bands within which most of the V values for a given character lie. There is much greater intraspecific varia-

Fig. 4. A comparison of the range of V values for each individual character as opposed to those for each species.

tion of non-homologous V's than interspecific variation of homologous V's, including even species of both subfamilies (fig. 4). For example the magnitude of V (including the species of both subfamilies) ranges only from 5.02 to 8.43 for Zy_W, from 4.23 to 6.72 to $M^3{}_L$, and from 3.48 to 5.87 for $IMol_L$. The coefficient of correlation between the mean V's for homologous traits in the 2 subfamilies is + .86. Conversely, the range of V's within a single species is from 2.63 to 15.96 for *M. (Met.) relictus* and from 3.31 to 15.89 in *M. matthewi*. The mean range of V values within each species is 9.42 as compared to 4.64 for each character. The mean range for dental characters is 3.27. The measurements on species with a low range of V (e.g., *B. buwaldi*) have been made chiefly on the teeth. It would appear, then, that the factors peculiar to the character itself have a greater influence on the magnitude of variation exhibited than factors common to all the characters within a given species. This might be expected in closely related lineages, such as the oreodont subfamilies here under discussion, in which the kinds and frequencies of the alleles governing the various characters had not departed radically from each other. More distantly related groups would be expected to show a lower correlation of V values for homologous characters. In a few cases, this similarity in variation of homologous characters between closely related species may be due to post-mortem factors. Thus it is not surprising to find that the variation in width of the skull (Zy_W) is greater than the variation in its length (Bas_L) in nearly every species (table 1) due to the greater effects of distortion on the former, even though measurements were not taken on badly distorted material. The differences in variation between characters of the same species should reflect a difference in the genetic variability of the characters concerned, if we assume that there has been no important differential in the environmental component of said variation. It is, of course, impossible to estimate how much of the variation here measured has a genetic basis. Little progress has been made in this regard even in skeletal studies of extant forms. A group of rodents (e.g., rats, mice or guinea pigs) in which a high degree of homozygosity had been attained through intense inbreeding or forms such as the nine-banded armadillo which regularly give birth to identical quadruplets, would make excellent material for a study of variation in the skeletal system in which the hereditary factor would be negligible or greatly reduced.

The variation in the dental characters is somewhat below the mean for the non-dental characters which may to a minor degree be a reflection of the negligible distortion in the former. Otherwise, there is little correlation between variation and topographic area of the skull. The mean variation in the mandible is somewhat below that of the skull but this can be attributed simply to the greater proportion of mandibular measurements that involve the teeth.

Rates of Change

The rates of change of the 23 unit characters derived by the use of the formula suggested by Haldane (see above) are given in table 4. In the Merycochoerinae the range of rates is from 8.03% per million-years (Pal_c) to 1.15% per million-years (Occ_W). The median for this subfamily is 2.04%, the mean 2.41%. All of the values with the exception of that for F_{10} are negative, i.e., the structures were decreasing somewhat in size. In the Merychyinae the range is from 3.13% per million-years (Occ_W) to 0.30% per million-years ($P^4{}_W$). The median in the Merychyinae is 1.35%, the mean 1.41%. All of the values are positive. A comparison of the two subfamilies reveals that the Merycochoerinae had a greater rate (ignoring direction of change) in 19 of the 23 attributes studied. The difference between the mean rates of the two

groups is 1.00% which is significant at the $< .01$ level of confidence. This differential in rapidity of change is reflected in the taxonomy of the groups; the Merycochoerinae are represented by two genera in approximately 9 million-years, the Merychyinae by only one genus in 12 million-years.

The medians for these oreodont subfamilies are considerably below 4.0% per million-years, the median figure given by Haldane (1949) for rates of change in ectoloph length, paracone height, and their ratio (a measure of hypsodonty) in the horse lineage. This quantitative approach thus confirms what students of Tertiary mammals had established on a qualitative basis, i.e., that equid evolution as a whole took place at rates considerably faster than the oreodonts, and in the case of the Merychyinae, more than twice as fast. Nevertheless, many individual oreodont characters evolved at rates equal to or greater than those of the Equidae. The figures for rates of change in the oreodonts are actually more comparable in magnitude to those of the dinosaurian suborders as given by Haldane. Here the range was from 6.1% to 0.26% with a median of about 2% for the rate of change in body length.

Relationship Between Variability and Rates of Evolution

The distribution of the 23 characters with regard to the relationship between variability and evolutionary rate of change in the two oreodont subfamilies is given in table 5. There are four possibilities for each of the characters studied: the Merycochoerinae (line 1) could have had the higher rate of change and also the greater variation (symbolized as category 1–1 in Table 5); the rate and variation for a given character could both have been greater in the Merychyinae (symbolized as category 2–2); the rate could have been greater in line 1 (Merycochoerinae) and the variation greater in line 2 (symbolized as 1–2) or the rate could have been greater in line 2 (Merychyinae) and the variation greater in line 1 (symbolized as 2–1). The distribution is far from random with 18 of the 23 characters in the 1–2 category. In a total of 20 cases (category 1–2 plus category 2–1) the lineage with the greatest evolutionary rate has the lowest variability. This departs significantly from randomness at the $< .01$ level of confidence in both the chi-square and sign tests. Can theoretical support be marshalled for such an association or must the correlation be disregarded as spurious? In the following discussion an attempt is made to evaluate some of the factors that may affect variation, evolutionary rates, and the relationship between the two.

Table 5. *Distribution of the 23 metric characters as regards relation between variation and rate of change in the Merycochoerinae and Merychyinae.* (Symbols for categories explained in text.)

Category	1–1	2–2	1–2	2–1
Frequency	1	2	18	2

No attempt has been made to discuss all of the factors that might have pertinency here, but rather to critically examine those evolutionary constituents which may have played a major role. Particular emphasis is placed upon those which have acted differentially in the two subfamilies. A more comprehensive treatment of these and other evolutionary determinants can be found in Carter (1951) or Simpson (1953).

Relative position in group history. Sloss (1950) concluded, after analyzing time-taxonomic frequency curves in several groups of marine invertebrates, that the pattern of such curves follows that of a normal probability curve. This would be a discovery of tremendous import, if true, since the evolutionary rate of a population at a given time would be a function of its relative position in the total group history. This would impose a degree of determinism which probably Sloss did not intend. As a preliminary

check of the possibility of such a relationship, the present writer constructed time-taxonomic frequency curves for the six reptilian subclasses as well as for three of the best-known orders of mammals—the carnivores, perissodactyls and artiodactyls. The genus was the taxonomic unit chosen for the analysis. There was no close approximation to the symmetrical normal curve in any group other than the obvious fact that all began from zero, reached a zenith, and approached or reached zero again. There was often bi- or trimodality with extreme skewness in the curves. Actually the approach of the graphs of Sloss to normality was only of this same very general nature.

Perhaps the inception of the oreodonts in the Eocene involved typogenesis (Schindewolf) or explosive evolution (Zeuner) or quantum evolution (Simpson); however, the Miocene oreodonts here under discussion are clearly evolving at slow horotelic rates primarily involving adaptive, cumulative changes to moderate shifts in the environment, a mode of evolution which Simpson (1953) has called phyletic. Although known descendants of the Merycochoerinae and Merychyinae are lacking, in neither group are there any overt clues as to why it should have become extinct at the end of the Miocene. Critical evidence on this point will perhaps never be obtained, but both groups would appear to be definitely under selective control and just as well adapted in the late as in the early members of the line. The less well-known Pliocene groups may possibly contain forms which are descendants of one or both of these subfamilies. In any event, the two subfamilies represent comparable stages in the history of the oreodonts as a whole; and any resulting conditions stemming therefrom should have acted indiscriminately on both phyletic lines.

Mutation rate. In theory, variability should be positively correlated with mutation rate. The genetic component of V in studies of fossil material is, of course, indeterminate. Actually, lack of information concerning mutation rate is not a serious limitation to the present analysis since there is, in all bisexually reproducing species, a tremendous store of potential genetic variability whose expression (as reflected in the measured variation) is probably more dependent upon selection than on mutation rate or any other one factor. Thus a bisexually-reproducing species which has 10 alleles at each of 1,000 loci (a conservative estimate for many, if not most, vertebrate species) has a potentiality of 10^{1000} different homozygous genotypes. Space limitation, if nothing else, would prevent the full expression of this potential. The differences in variation as found between the two oreodont subfamilies can be most reasonably ascribed to a factor controlling the release of the potential variability (*i.e.*, selection) rather than to a disparity in mutation rates between the two lines.

The relationship between mutation rate and evolutionary rate is even more obscure. It might be expected that lineages evolving at rapid rates would exhibit higher than usual rates of mutation. Actually, there is no direct evidence on this point. Wright (1940) has shown that in some special circumstances (e.g., very small populations) evolutionary rate may vary directly with the mutation rate. In most lineages, including the Merycochoerinae and Merychyinae, mutation rate almost certainly is not a limiting factor for rate of evolution.

Population size. Contemporaneous intragroup variation tends to be proportional to population size; however, there are limits above which a further increase in size of population brings about virtually no further variability increase (Wright, 1931). Under usual circumstances, this critical level is approximately $1/4s$ (where s = coefficient of selection). With $s = .0001$ (extremely low selection pressure), the critical population size above which there would be little variability increase due to size alone would only be 2,500.

The effectiveness of selection tends to vary directly with the size of the population. Selection will be effective if $s > 1/4N$ (Wright, 1931). Thus if $s = .001$ (a selection coefficient far below that demonstrated in experimental studies), selection should be effective in populations of 250 or more. Below this level, random sampling effects (genetic drift) will have a greater influence on the change in gene frequencies.

Although estimation of the size of populations long extinct is at best a hazardous undertaking, it is reasonably certain that the oreodont subfamilies had population sizes consistently numbering in the several thousands. The Merycochoerinae probably had somewhat smaller populations than the Merychyinae (as reflected in the numbers collected and assuming that the probability of fossilization and subsequent recovery was approximately equal in both lines). Nevertheless, it is a safe assumption that both were well above the level at which a size increase in and of itself have materially increased the variability. Any differential in population size would not have accounted for the demonstrated disparity in variabilities between the two groups. It is also reasonable to assume that selection was very effective in both groups and that the effects of random sampling from generation to generation played a minor role in changing gene frequencies. Genetic drift could, of course, have played an important role if the species were composed of partially isolated subgroups; here the critical evidence as to the population structure of the various species is unknown.

Length of generation. The rate of evolution of animal groups should vary inversely with the average length of generation since almost all events having evolutionary significance take place between rather than during generations. In practice so many exceptions have been found to the above (e.g., the classic comparison of didelphids and proboscidea), that it has been seriously doubted if there is any cause-and-effect relationship here at all. The relationship probably exists but its effect is small and usually obscured by other more dominant factors. It could be demonstrated by comparing 2 lineages in which all other factors were held constant, an unrealized ideal at present. Although not directly determinable, the mean length of generation in the Merychyinae and Merycochoerinae was probably in the order of 3 years, i.e., similar to sheep, goats, and pigs, their closest living counterparts in size and habits. Since length of generation is in a general way proportional to body size, it might be expected that the Merychyinae would have had somewhat shorter generations, which may be reflected to a minor extent in its evolutionary rate when compared with the Merycochoerinae. The median evolutionary rate per generation would be about 6.0×10^{-8} in the Merycochoerinae, about 4.0×10^{-8} in the Merychyinae. Haldane (1949), gives 2×10^{-7} as the median rate per generation in the horse phylum.

Selection. For groups in the phyletic mode of evolution, variability tends to vary inversely with intensity of selection. Adaptive structures, playing an important role in the functional economy of the organism, have a lower variability on the average than non-functional structures not under rigid selective control. The high variability in such degenerating, non-functional structures as the wisdom teeth of man or the canines of the horse is well known. For some exceptional groups, very well adapted to a relatively stable environment (i.e., at or near an adaptive peak in Wright's model), increased selection may almost completely halt what evolutionary progression was taking place. In the much more common case, where the population is fairly well down the slope of the adaptive peak, increased selection should increase the rate of change of gene frequencies. Thus, in the first example, evolutionary rate would vary inversely with selection pressure; and, in the second case, it would vary directly with selection pressure. In both of these

examples increased selection would tend to reduce variability.

Selection appears to be the factor, which is acting in a differential fashion on the two oreodont subfamilies, producing greater rates and lower variability in the one and lower rates with greater variability in the other. As discussed above, the population size in both subfamilies is adequate for selection to be effective and for random effects to be reduced to a minimum. Both subfamilies have rather low but appreciable rates, implying that they are continually "chasing" a slowly changing environment.

Thus the form under greatest selection pressure (Merycochoerinae) should be changing at the greater rate and exhibit the lower variability (fig. 5).

The Merycochoerinae were changing at this time from a plains form to one with at least partially-aquatic habits. The most obvious change during this time, other than the development of the proboscis, was a decrease in size of the creatures. This may have been adaptive under these circumstances. Each individual difference in rate and variability between analagous characters within a species or between homologous characters between species cannot be explained as due to greater or lesser selection because of the obvious impossibility of ascertainment of selection values for each character.

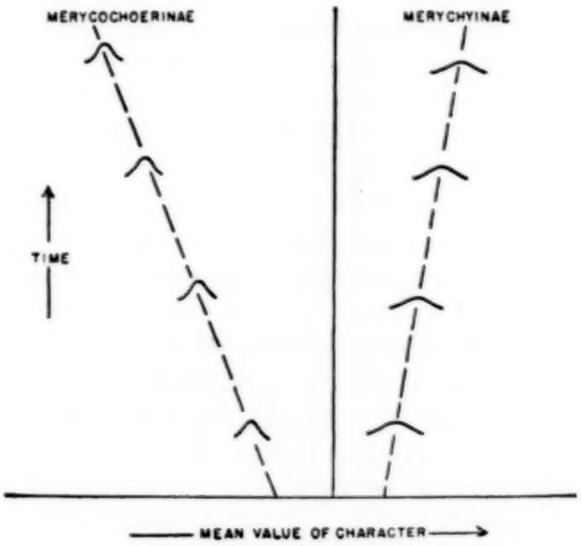


FIG. 5. A schematic representation of the relationship between variability and evolutionary rate in the two oreodont subfamilies. The Merycochoerinae are evolving more rapidly and exhibiting less contemporaneous intragroup variability than the Merychyinae. Slope of lines is proportional to evolutionary rate, being positive in the Merychyinae and negative in the Merycochoerinae.

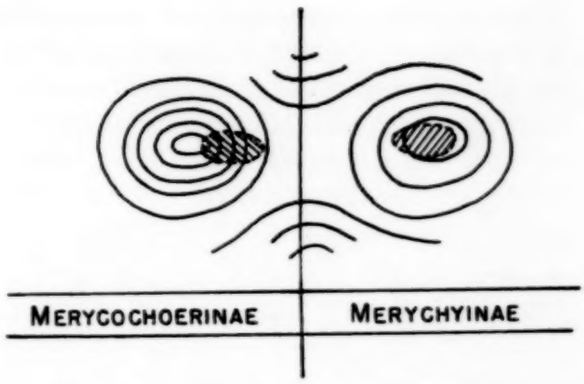


FIG. 6. A pictorial representation of the two oreodont subfamilies on an adaptive grid. (Explanation in text.)

As pictured on Wright's adaptive grid (fig. 6), both subfamilies would be on the slope of an adaptive peak, with the Merycochoerinae going up a somewhat steeper incline, indicative of greater selection pressure.

In preliminary work for the present study, the coefficient of variation was obtained for five modern species of mammals. These included 3 species of opossums (*Didelphis*), 1 squirrel (*Sciurus*), and 1 South American rodent (*Dasyprocta*). The size of the samples varied from 50 in *Sciurus* to 20 in the *Didelphis*. The opossums have probably had a more conservative history than any other living mammalian group while the rodents have evolved at definitely more rapid rates. The mean V for 16 metric characters of the skull in each of the species is as follows:

Didelphis marsupialis virginiana	8.75
Didelphis marsupialis marsupialis	8.63
Didelphis azarae pernigra	7.00
Dasyprocta fuliginoga	5.05
Sciurus rufus niger	4.04

These results, although not conclusive in themselves, do lend further support to the general thesis that more rapidly evolving groups may have lower variability.

Conclusion

Simpson (1953) suggested that extremely rapid evolution should be accompanied not by high but by very low intragroup variability. He set up a hypothetical model in which a series of progressive mutations occur at one locus. One mutation occurred per generation and the selective value for the new mutant was 100%. Each successive mutant is "run through" the population in just 3 generations. This extremely rapid evolution is accompanied by intragroup variability which is extremely low; in fact, it consists of only two genotypes at any one time—that possessed by the group as a whole and that of the individual which bears the new mutant.

Although admittedly departing widely from this highly theoretical model in complexity, natural populations should approach this ideal form as an upper limit. Such appears to be the case in the two oreodont subfamilies under discussion. In the Merycochoerinae, alleles (under stronger selection pressure) are pushed through the population faster, resulting in a more rapid change in gene frequency (or a greater evolutionary rate, which is the same thing). A more homozygous group is thus produced with a consequent lowered variability.

It should also be pointed out that there is a certain amount of bias working against the results obtained, due to the manner in which the population samples were obtained. Each species has been treated as if made up of contemporaneous individuals; thus intraspecific variation has been considered contemporaneous intragroup variation. Since we are dealing with a phyletic progression, each of these "vertical" species represents evolution over about a 2 million-year span. In the Merycochoerinae, the more rapidly evolving group, part of the intragroup variation is actually successive intergroup variation. In the Merychyinae with a slower rate of evolution, there would be less change within a species and thus the variation as measured is more nearly contemporaneous intragroup variation. This illustrates the fact that the differences in contemporaneous intragroup variation between the two subfamilies is actually greater than that indicated by the data. Evidence has been adduced to show that significant differences in variation and evolutionary rate exist between the two subfamilies, and the hypothesis that both factors are linked through the differential effect of selection intensity in the two lineages is proposed as the most reasonable postulate explaining this relationship. However, work on other lineages (probably other Tertiary mammals for the most part) must determine the scope of this relationship in other groups. A search of the literature yields no other study in which two phyla evolving through the same time span have been studied in this respect.

Studies of this nature, i.e., those dealing with the evolutionary dynamics of fossil populations, must necessarily be of a strongly inferential type. Only by recourse to perhaps the most important principle of the paleontologist, that of biological uniformitarianism, can we hope to gain an insight into the mechanics of evolutionary change in groups in which the changes have been of a major scope, i.e., in fossil populations. Population size, length of generations, selection pressure, and variability are all variables whose interrelationships must be ascertained from the study of neozoological material before analyses which are above the level of mere speculation can be attempted on paleozoological material.

The present work has not escaped weaknesses which are perhaps congenital to studies of this sort. The conclusions drawn would have a somewhat greater validity if the sample size of most of the species of the Merycochoerinae had been

larger. Although very abundant as a group, even the oreodonts do not always present an adequate statistical sample in every character when broken down to the specific level. Secondly, quantitative studies of this sort can, of course, never be more valid than the taxonomy on which they are based. Probably the optimum conditions for a valid taxonomy from which to work are found where abundant material has been recently monographed by veteran workers who possess a detailed knowledge of the stratigraphy as well as the fossil groups. Such have been the conditions under which the classification of the Merycochoerinae and Merychyinae have been carried out. Finally, a better understanding of the organismic-environmental relationship, a great deal of which must remain conjectural at present in the two subfamilies, is much to be desired.

Summary

This study is concerned with the evolutionary rate and the variability in two subfamilies of oreodonts, an extinct group of Tertiary mammals. The two subfamilies, the Merycochoerinae and the Merychyinae, evolved through approximately the same Middle to Late Miocene sequence, a span of about 12 million-years. The Merycochoerinae are considerably larger, with rather pig-like proportions and a reduction of the nasal bones indicative of a tapir-like proboscis. The habitat, at least in the later members of the line, was probably semiaquatic. The smaller group, the Merychyinae, were extremely conservative, lightly built forms with bullet-like heads. They remained plains-dwelling, cursorial forms throughout the sequence. The geographic setting is The Great Plains area of western Nebraska, eastern Wyoming, southwestern South Dakota, and northeastern Colorado.

Twenty-three measurements were made on the 5 species of each subfamily. Variability was measured by the Pearsonian coefficient of variation. Evolutionary rate was given as a mean percent change in each unit character per million-years.

In neither subfamilial lineage is there a marked secular trend in the magnitude of the variation. An analysis of the variation in 3 species of the Merychyinae demonstrates an important interrelationship between variability and speciation. A large, widespread, highly variable species, *M. minimus*, gave rise to *M. arenarum* by the process of speciation. *M. elegans*, the direct descendant of *M. minimus* through phyletic progression, and *M. arenarum* both show significantly less variation than the parental population, *M. minimus*. Part of this reduced variability is later restored in the *elegans* line. In comparing the two subfamilies, the Merychyinae have the higher mean variation in 20 of the 23 characters studied.

The evolutionary rates are considerably below comparable figures for metric characters in the evolution of the horse. The Merycochoerinae have a greater rate than the Merychyinae in 19 of the 23 characters examined. This difference is statistically significant.

In 18 of the 23 characters the Merycochoerinae evolved at the more rapid rate while the Merychyinae exhibit the greater variability in the same traits. Evolutionary factors which may have played a role in this relationship are discussed. These include relative position in the history of the group, mutation rates, length of generation, population size, and selection. It is concluded that the greater intensity of selection on the Merycochoerinae is the principal factor accounting for their greater evolutionary rate and lower variability.

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COMPARATIVE PHYSIOLOGY OF SOME CHROMOSOMAL TYPES IN *DROSOPHILA PSEUDOOBSCURA* [1, 2]

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INTRODUCTION

Chromosomal polymorphism, in the form of simultaneous occurrence of two or more inversion types, is a widespread phenomenon in natural populations of *Drosophila pseudoobscura*. Dobzhansky and co-workers have carried out extensive field and laboratory studies on various local populations of this species. At Piñon Flats on Mount San Jacinto in California, two common gene arrangements in the third chromosome, Standard (ST) and Chiricahua (CH), exhibit seasonal cycles. CH increases at the expense of ST in spring, and the reverse trend occurs during summer (Dobzhansky, 1943), suggesting that in nature these karyotypes are subject to selection pressures.

In the laboratory, population cage experiments carried out on flies of Piñon Flats extraction showed that different initial proportions of ST and CH inversion types approached a characteristic equilibrium frequency of about 75% ST and 25% CH at 25° C. (Wright and Dobzhansky, 1946; Dobzhansky, 1947; Dobzhansky and Pavlovsky, 1953). At 16.5° C. no significant change from the initial frequency was observed. The occurrence of a characteristic equilibrium at 25° C., rather than elimination of one of the two chromosomal types, indicates that the structural heterozygote ST/CH has an overall adaptive advantage over both homozygotes, ST/ST and CH/CH, under the conditions of the experiment. From the most recent experimental data, adaptive values have been calculated at ST/CH = 1.00, CH/CH = 0.413, and ST/ST = 0.895 (Dobzhansky and Pavlovsky, 1953).

Some attempts to discover the physiological properties of the flies which may be responsible for these differences in adaptive values have been reported (Heuts, 1947 and 1948; Levine, 1952). Heuts found a differential longevity at 0 to 4° C. and at 28 to 30° C. Levine compared CH/CH, ST/ST, and ST/CH flies with regard to the effects of temperature and relative humidity on developmental and adult stages. It should be noted that in Levine's work efforts were made to raise the experimental material under optimal conditions in all cases. With his technique, no differences in the performance of egg or larval stages were observed. At some temperatures and relative humidities, differences were found in pupal viability and in the ability of adults to survive starvation. In every case of demonstrated difference, CH/CH proved least viable with ST/ST either equal or superior to ST/CH. No evidence for any superiority of the heterozygote was found.

The work reported here is an attempt to discover some of the reasons for the overall adaptive advantage of the ST/CH heterozygotes by making physiological comparisons among the three karyotypes. A deliberate attempt was made to raise the experimental material under conditions more nearly approximating those in the crowded population cages. With limited environmental resources, the amount

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[2] Part of this study was conducted during the tenure of a fellowship from the National Cancer Institute of the National Institutes of Health, Public Health Service.

of variability among individuals would be expected to be great since competitive conditions would tend to differentiate the less fit from the more fit. The experimental results bore out this expectation.

The traits chosen for study were fecundity, longevity in the presence of food, and percentage emergence of adults from larvae raised under crowded conditions.

Apart from these physiological traits, there is another characteristic which has been considered to be of importance in evolution. Homeostasis has been defined as the ability of an organism to continue functioning normally in spite of environmental diversity. In a population in which natural selection had achieved a delicate adjustment of individual physiological traits to secure a maximum fitness of the whole population in the normal range of environments, homeostasis would be expected to confer upon its possessors considerable adaptive advantages. As a measure of relative degrees of homeostasis, comparisons were made of the amounts of variation within each chromosomal type with respect to every character studied.

Materials and Methods

Seventeen strains homozygous for the ST gene arrangement and thirteen for the CH arrangement, each derived from a single fly collected at Piñon Flats, California, were used. To prepare the experimental material, the original stocks of ST/ST and of CH/CH were each separated into two approximately equal groups. Structurally homozygous ST/ST individuals which were at the same time genically heterozygous were obtained by mating virgin females isolated from one group of ST stocks to males collected from the other set. CH/CH individuals were obtained similarly. ST/CH heterozygotes were secured by mass-mating virgin females from all strains of one karyotype to males of all strains of the other karyotype. In this way, not only was each fly genically heterozygous, but within each chromosomal type there was genetic diversity among individuals.

Because the adaptive differences between the chromosomal types are known to occur under competitive conditions, an effort was made to raise the experimental material under similar conditions. For the longevity experiments, mass-matings of 20 females and 20 males were made in half-pint milk bottles containing lightly yeasted cream of wheat-molasses food. Every 3 to 4 days, when the food had become well tunneled with larvae, the parental flies were transferred to fresh bottles. The earliest emerging flies were discarded, and only individuals emerging after the third day were used for experimental purposes since the early flies probably had better than average conditions for development. For the fecundity experiments, mass-matings of approximately five hundred flies of each sex were made in population cages. When food cups became crowded with larvae (about 4 or 5 days) they were removed from the cage and isolated under glass chimneys plugged with cotton. In this case also, only flies emerging after the third day were used.

Fecundity

To secure material for the fecundity experiments, three population cages were set up as described above, one to yield ST/ST flies, another CH/CH, and a third ST/CH heterozygotes. For the experimental unit, five newly-emerged females of one chromosomal type and ten males of the same type were placed together in a 1 × 4 inch glass vial containing a paper spoon with a small amount of cream of wheat-molasses food moistened with a drop of thin yeast suspension. Experiments were conducted at 25° C. and 16° C. Spoons were changed and the eggs counted under a binocular microscope every day for the 25° C. series, and every other day for the 16° C. series, until no females remained alive. Males were replaced as they died so that egg-

TABLE 1. *Fecundity measured in eggs per surviving female per day, averaged over ten day intervals. 25° C.*

	ST/CH	CH/CH	ST/ST	Significant differences
Exper. A	*4 vials*	*4 vials*	*5 vials*	
0–10 days	9.04±0.47	11.89±1.26	14.17±1.29	ST/ST>ST/CH at .05
11–20 days	17.48±1.23	17.07±1.42	18.22±1.23	none at .05
21–30 days	10.67±0.49	12.32±2.68	15.65±2.61	none at .05
31–40 days	11.90±1.77	5.67±2.66	8.68±3.88	none at .05
41–50 days	8.20±1.94	1.58±0.69	3.34±1.79	ST/CH>CH/CH at .05
51–60 days	2.88±1.20	0.18±1.97	0.78±0.65	none at .05
61–70 days	1.28±1.08	0	0	none at .05
Exper. B	*9 vials*	*10 vials*	*10 vials*	
0–10 days	23.05±1.05	19.92±1.69	22.87±1.74	none at .05
11–20 days	32.18±1.91	31.51±2.93	35.76±2.89	none at .05
21–30 days	32.53±1.93	21.08±2.86	34.20±2.20	ST/CH>CH/CH at .01 ST/ST>CH/CH at .01
31–40 days	17.10±1.89	10.09±2.69	20.32±1.73	ST/ST>CH/CH at .01
41–50 days	10.63±2.53	3.74±1.29	16.61±2.66	ST/CH>CH/CH at .01 ST/ST>CH/CH at .01
51–60 days	3.33±0.91	0.74±0.41	5.00±1.59	none at .05
61–70 days	0.14±0.13	0.06±0.07	1.28±0.48	none at .05

laying would not be influenced by a scarcity of males.

At 25° C. two fecundity experiments were performed; since they gave somewhat different results, they will be considered separately. The data are summarized in tables 1 and 2. The number of eggs laid in Experiment A was approximately half those laid in Experiment B. Experiment A was carried out one year earlier than B; during this time changes in the experimental conditions may have occurred. Moreover, the large variances and the small number of replications, especially in Experiment A, make some of the apparent differences statistically insignificant. (In testing for significance, the following method was employed: An analysis of variance was performed on the total data. If this yielded a significant F value, t tests were carried out on each pair of mean values.) Experiment B (see table 2) indicates that in total number of eggs per female per lifetime (which includes the effects of both fecundity and longevity) ST/CH

TABLE 2. *Overall fecundity*

	ST/CH	CH/CH	ST/ST	Significant differences
Eggs per female per lifetime				
25° C. Exp. A	556±36	381±56	507±69	none at .05
25° C. Exp. B	1054±63	735±79	1227±106	ST/CH>CH/CH at .01 ST/ST>CH/CH at .01
16° C.	548±50	324±56	489±64	ST/CH>CH/CH at .05
Eggs per surviving female.				
16° C.	610±42	502±70	714±93	none at .05

TABLE 3. *Longevity: Average length of life in days*

	Longevity experiment				Fecundity experiment	
	16° C.		25° C.		16° C.	25° C.
	females	males	females	males	females	females
ST/CH	156.8±3.5	126.7±2.8	63.4±2.9	58.2±3.4	112.0±8.5	51.6±1.3
CH/CH	143.5±4.2	121.1±4.2	56.2±1.3	51.4±1.8	74.2±11.8	34.6±6.5
ST/ST	128.8±9.1	115.5±5.6	57.1±3.1	52.3±3.1	93.1±11.9	36.2±2.4

heterozygous females are similar to ST/ST homozygotes, and both are superior to CH/CH females. Similarly, in eggs per day per surviving female (fecundity alone) CH/CH females are inferior. The results of Experiment A are less clear cut, but on the whole confirm the combined effects of fecundity and longevity found in Experiment B.

The low egg production in the early periods of the ST/CH females relative to that of the two homozygotes in Experiment A as compared with Experiment B may be the result of differences between reciprocal crosses. In Experiment A, ST females were crossed with CH males to secure the ST/CH heterozygotes, while in Experiment B, CH females and ST males were used as parents. Spiess (1954) found a similar maternal effect in the early egg-laying period of certain structural heterozygotes of *D. persimilis*.

To measure fecundity at 16° C. nine vials of each chromosomal type were run. The results are summarized in table 2. Although the differences in mean number of eggs produced per lifetime (row 3) seem to be great, because of the large variances these results have a probability of occurrence by chance of only slightly less than 5%. The effect of differential longevity can be removed by dividing egg production into periods between deaths of females. The total number of eggs produced during each period is then divided by the number of females surviving during that time. These results are then summed for the entire egg-laying span (row 4). When these operations are carried out, the differences in means are no longer significant.

LONGEVITY

The experimental flies were raised in crowded half-pint bottles as described above. Twenty-five of each sex, aged less than 24 hours, were placed together in fresh bottles with approximately ½ inch of lightly yeasted cream of wheat-molasses food and stored in a constant temperature room either at 25° C. or at 16° C. At the higher temperature, the bottles were changed and the flies counted every three to four days. At 16° C. the changes were made once a week. Due to accidental losses, the completed experiment contained 10 ST/CH, 9 CH/CH, and 9 ST/ST bottles at 25° C. and 7 ST/CH, 9 CH/CH, and 7 ST/ST bottles at 16° C. The average length of life is given in table 3.

In every case, ST/CH flies lived longer on the average than homozygous flies of the corresponding sex. However, because of large variances relative to the differences in the means, only the data for females at 16° C. show statistically significant differences at the 5% level.

Further data on longevity in females come from the fecundity experiments, where a record was kept of the date of death of each egg-laying female. The information on average longevity from these experiments (table 3) confirms the greater length of life of ST/CH females. (At 16° C. the average longevity of ST/CH females in significantly higher than CH/CH at the .05 level. At 25° C. the average longevity of ST/CH is significantly higher than that of ST/ST.) The actual longevities are, of course, different in the fecundity and longevity experiments because of the considerable difference in the environments.

Neither of these experiments reproduces very closely the conditions of life of *D. pseudoobscura* either in nature or in a population cage. However, they do indicate that, under some circumstances, ST/CH heterozygotes tend to live longer.

Larval and Pupal Viability

The method used in these experiments is analogous to that of Vetukhiv (1953). Five types of matings were made: 1a) ST/ST virgin females × CH/CH males; 1b) CH/CH virgin females × ST/ST males; 2) ST/ST virgin females × ST/ST males (of other stocks); 3) CH/CH virgin females × CH/CH males (of other stocks); and 4) mutant orange *D. pseudoobscura* females × orange males. Females were allowed to oviposit for 24 hours on spoons of yeasted cream of wheat-molasses food at 25° C. Small vials containing 4 cc. of Kalmus synthetic food (Kalmus, 1943) were yeasted with 0.1 cc. of a 14% suspension of dry Fleischmann's yeast. Newly hatched larvae of known origin were placed on the surface of the food. The vials were then stored at 25° C. until the emergence of adults.

For the first set of experiments, ten larvae of one experimental type (ST/CH larvae were chosen at random from 1a and 1b matings) and ten orange larvae were placed in each vial. (The orange larvae were introduced as a control on the experimental conditions and to provide the competition of another larval type.) Adults were counted daily as they emerged.

Two experiments containing a total of twenty vials of each type gave similar results and will be considered together (A). Experiment B (10 vials of each type) used softer food and gave different results. Average emergence of wild-type (i.e. experimental) larvae and of their orange controls is given in table 4.

Because a larval density of 20 allowed such a high total emergence rate of wild-type flies, further experiments were set up to test the effect of more stringent conditions. For each chromosomal type, 80 vials were prepared, containing 15 wild-type and 15 orange larvae (C). The results of these experiments are summarized in table 4.

Experiment B indicated that there are certain conditions in which significant differences in the mean number of emerging adults can be found. In this experiment an unfavorable medium has caused differential mortality. Experiment C provides further information on the effects of crowding. (The significantly higher mean emergence of orange in the presence of the inferior CH/CH as compared with orange accompanying ST/CH or ST/ST indicates that a larval density has been reached where competition has become a factor.)

These experiments represent an extremely small sample of the possible sets of conditions under which *Drosophila*

Table 4. *Larval and Pupal Viability: Mean number of adults per vial. 25° C.*

	ST/CH	CH/CH	ST/ST	Significant differences
A. 20 vials				
wild type	9.35±0.19	8.75±0.23	8.60±0.36	none at .05
orange	6.10±0.45	5.30±0.45	5.65±0.44	none at .05
B. 10 vials				
wild type	4.70±0.33	2.80±0.37	6.50±0.49	ST/CH>CH/CH at .05 ST/ST>CH/CH at .05
orange	5.50±0.65	5.10±0.41	5.50±0.48	none at .05
C. 80 vials				
wild type	9.17±0.45	5.20±0.96	10.61±0.58	ST/CH>CH/CH at .01 ST/ST>CH/CH at .01
orange	3.01±0.37	4.88±0.44	3.73±0.14	CH/CH>ST/CH at .05 CH/CH>ST/ST at .05

TABLE 5. *Rate of development: mean length of larval and pupal life in days. 25° C.*

	ST/CH	CH/CH	ST/ST	Significant differences
A. 20 vials	13.57±0.07	13.82±0.07	13.64±0.07	ST/CH <CH/CH at .01
B. 10 vials	13.92±0.17	14.82±0.24	14.63±0.15	ST/CH <ST/ST at .01 ST/CH <CH/CH at .01
C. 80 vials	12.97±0.03	13.01±0.03	13.22±0.03	ST/CH <ST/ST at .01 CH/CH <ST/ST at .01

pseudoobscura larvae could be raised, using the same general method. The total number of larvae, the type and number of competing larvae, as well as the medium itself, could be varied in a large number of ways to yield further information on the range of performance of larvae bearing ST and CH chromosomes. Yet none of these possible experiments will duplicate conditions in a population cage, where larvae of all types and ages develop together in a seething mass, only a very small proportion of which reaches adulthood. Therefore, the results of these experiments can be considered to indicate the performance of the larval types only under the specified conditions, and extrapolations should be made with caution.

RATES OF DEVELOPMENT

Since daily records of emergence numbers were kept for the viability experiments, rates of emergence of the three kinds of wild-type flies could be calculated. The results of these analyses are summarized in table 5. In every case, ST/CH showed a significantly shorter developmental period than at least one of the homozygous types. In these experiments, the absolute differences are not great. However, it is not unreasonable to suppose that in the much more crowded population cage cups these differences would be accentuated.

COMPARISON OF VARIANCES

An examination of the variances exhibited by each of the three chromosomal types in the course of the different experiments suggested a definite tendency for the structural heterozygote ST/CH to show a lower variance than either of the homozygotes (see table 6). To test this observation statistically, Bartlett's method for testing for homogeneity among variances (see Snedecor, 1946, pages 249–251) was employed.

When this test was applied to the experimental variances, the differences proved to be statistically significant (.05 level) in only four out of twenty indi-

TABLE 6. *Summary of variance data.* (Variances are relative, that of ST/CH being arbitrarily set at 1.00.)

Source	Variance CH/CH	Variance ST/ST
Longevity 16° C. ♀ ♀	1.56	6.06
Longevity 16° C. ♂ ♂	2.01	3.76
Longevity 25° C. ♀ ♀	0.36	1.17
Longevity 25° C. ♂ ♂	0.51	0.85
Longevity 16° C. ♀ ♀ (fecundity data)	1.90	1.94
Longevity 25° C. ♀ ♀ (fecundity data)	23.49	5.06
Fecundity 25° C. A		
0–10 days	7.06	9.31
11–20 days	1.32	1.24
21–30 days	29.84	35.14
31–40 days	2.38	6.11
41–50 days	0.12	1.06
Fecundity 25° C. B		
0–10 days	2.57	2.71
11–20 days	2.64	2.55
21–30 days	2.43	1.43
31–40 days	2.08	0.86
41–50 days	0.29	1.23
Fecundity 16° C.	2.80	4.93
Larval and Pupal Viability A	1.36	3.35
Viability B	1.12	1.48
Viability C	5.32	1.95

TABLE 7. *Comparison of variances*

Source	Chi square	d.f.	p
Longevity	23.286	12	.025
Fecundity	33.780	22	.050
Larval and pupal viability	16.432	6	.012
Total	73.498	40	.0005

vidual cases. But in the aggregate, the trend for ST/CH to show less variability proved unquestionably real ($p = .0005$). To make this analysis, Fisher's method for the combination of probabilities from tests of significance (see Fisher, 1948, section 21.1) was employed. In applying this test, if both homozygote variances were larger than that of the heterozygote, the difference was considered to be in the direction of the trend and ½ of p from Bartlett's test was used to compute Chi square. If either of the homozygote variances was smaller than that of the heterozygote, this was considered an exception to the trend and $(1 - p/2)$ was used. The analysis is summarized in table 7. Each of the three major components of the variance data is at or somewhat below the .05 level of significance. When these are combined, however, the probability of occurrence by chance drops to .0005. The biological significance of this relative homogeneity of the heterozygote will be considered below.

INDICES OF PERFORMANCE

The results of the present experiments can be combined, giving comparative indices of general performance for the three chromosomal types at 25° C. The feasibility of such an approach has been demonstrated by Wallace (1948), working with an X-chromosome inversion in *D. pseudoobscura*. He used an index of "selective value" calculated from separate longevity, fecundity, etc., experiments which gave values corresponding very closely to the "adaptive values" derived mathematically from population cage experiments. A similar method has been employed to combine the results of the present experiments. In the first section of table 8 the mean performances of the homozygotes in each experiment are expressed relative to that of the heterozygote, set arbitrarily at unity. In calculating the fecundity results, three different methods were employed: 1) the number of eggs per surviving female was obtained by summing the columns in table 1, thus removing the effects of differential longevity; 2) total fecundity was obtained by a summation

TABLE 8. *Summary of indices of relative performance. 25° C.*
(A and B refer to the two fecundity experiments conducted at 25° C.)

		ST/CH	CH/CH	ST/ST
I. Larval and pupal viability		1	0.567	1.157
II. Rate of development		1	0.997	0.981
III. Longevity of males		1	0.883	0.899
IV. Longevity of females		1	0.886	0.901
V. Fecundity (eggs per surviving female)	A	1	0.793	0.990
	B	1	0.733	1.144
	A+B	1	0.763	1.062
VI. Fecundity (total)	A	1	0.685	0.912
	B	1	0.697	1.164
	A+B	1	0.691	1.038
Overall Indices				
½{I×II[III+(IV×V)]}		1	0.440	1.054
½[I×II(III+VI)]		1	0.445	1.099
Mean of indices		1	0.443	1.077

of all eggs laid in the course of the experiments; 3) numerical weights were assigned to successive egg-laying periods in an attempt to take into account the fact that a female may continue to lay eggs for some time after her first daughters have begun their own egg-laying cycles. (Method 3 yielded numerical index values almost identical with those of method 2. Since the weights chosen were arbitrary, these results have not been included in the table.) It is interesting to note that, whatever the method of calculation, ST/CH females derived from ST/ST mothers seem to make up any initial deficiency in fecundity, so that an index based upon Experiment A differs very little from the corresponding index based upon Experiment B in which the ST/CH females were derived from CH/CH mothers.

Overall indices were calculated giving equal weight to contributions of males and females (see Wright and Dobzhansky, 1946). The methods of calculation are shown in table 8. Two indices based on the different measures of fecundity give an average value of 0.443 for CH/CH and of 1.077 for ST/ST as compared with the "adaptive values" of 0.413 for CH/CH and 0.895 for ST/ST as calculated from recent cage experiments (Dobzhansky and Pavlovsky, 1953). This agreement is probably as close as might be expected, considering that the experimental conditions are obviously not identical with those in population cages and also that only the most obvious components of "adaptive value" were tested.

Discussion

The results reported here are in general agreement with those of Levine (1952) since, in all cases where adaptive differences can be shown to occur, CH/CH homozygotes are inferior to both ST/ST and ST/CH. In addition, the data on longevity and on rates of development point to other sources of the adaptive superiority of the ST/CH heterozygote. The data on the survival rates in the pre-adult stages indicate a decided inferiority of the CH/CH homozygote under the conditions of most of the experiments. The ST/ST homozygote is, in the same environment, at least equal and possibly superior to the heterozygote. Yet Dobzhansky (1947) demonstrated that, under cage conditions, there is a differential mortality in the pre-adult period which favors ST/CH heterozygotes slightly over ST/ST homozygotes and greatly over CH/CH homozygotes. However, complete agreement would not necessarily be expected, since the conditions of the present experiments are, as previously noted, different from those in population cages. This difficulty in duplicating cage conditions does not invalidate the reality of differences which have been demonstrated experimentally, but it does make attempts at extrapolation hazardous. Nevertheless, an attempt may be made to combine the data from the different experiments to secure an estimate of overall performance for each of the three chromosomal types. The calculated average performances of the homozygotes relative to that of the heterozygote agree as well as can be expected with the adaptive values obtained from cage experiments.

Perhaps the most suggestive of the results obtained is the observation that the ST/CH heterozygotes exhibit a lower variability in the physiological characteristics studied than either of the homozygotes. Phenotypic variation may be caused by a genetic diversity among the individuals studied, by environmental factors, or by a combination of both. Genetic diversity was undoubtedly present in the populations on which the observations were made, since these populations were obtained by crossing several strains of flies (see above). There is, however, no reason to suppose that the genetic diversity was any greater among the structural homozygotes than among the heterozygotes. Indeed the same original strains were employed in both; if anything, the heterozygotes should be more variable than the homozygotes since they were ob-

tained by crossing all of the ST strains to all of the CH strains. Environmental variations were also present. The experimental populations were deliberately raised under conditions of crowding. In crowded habitats, some individuals accidentally secure more abundant food and more favorable places in which to live than do other individuals. But again, there is no reason to think that environmental variations were greater for homozygotes than for heterozygotes. We are forced to conclude that the observed differences in the variances indicate a greater uniformity of response to environmental diversity in ST/CH heterozygotes than in either of the homozygotes, ST/ST or CH/CH.

Several investigators have recently reported that, when exposed to the same variety of environmental stimuli, heterozygotes produce more uniform phenotypes than do homozygotes. Thus, Mather (1950), working with inbred lines of *Primula sinensis,* found that the developmental variation in the style length of flowers of the same plant is greater in the inbred lines than in their F_1 or even F_2 progeny. Robertson and Reeve (1952), measuring wing-length of inbred lines of *D. melanogaster* and their F_1 progeny, found that, on the average, inbred lines exhibit almost double the phenotypic variance of crosses between them. Similar results were reported by Wigan (1944) for the variability in the number of sternopleural bristles in *D. melanogaster,* by Mather (1953) for asymmetry in the number of sternopleural chaetae, and by Smith and Smith (1954) for rates of development in *D. subobscura.* Dobzhansky and Wallace (1953) studied the effects on the viability of the flies of homozygosis and heterozygosis for certain chromosomes derived from natural populations of *D. pseudoobscura, D. persimilis,* and *D. prosaltans,* and from experimental populations of *D. melanogaster.* In every species the survival rates of the homozygotes varied appreciably among replicates, while among the heterozygotes the variation was about as great as can be accounted for by sampling errors alone. The development of the heterozygotes is, on the average, better buffered against environmental disturbances than is the case in homozygotes. Dobzhansky and Wallace considered this phenomenon to indicate a superior homeostatic adjustment of the developmental pattern in an average heterozygote. Waddington (1953) reached essentially the same conclusion, but he uses the word "canalization" for homeostatic buffering of the developmental pattern.

All of the previous described cases of homeostasis concerned genic hetero- or homozygosity. The observations reported in the present article deal with a greater stability of structural heterozygotes and a greater variability of structural homozygotes. There is no fundamental difference between genic and chromosomal homeostasis, but the observations presented here help bridge the gap between the purely genetic and the cytogenetic work on Drosophila populations.

A large body of experimental work of the last few years makes it increasingly clear that, at least in sexual and cross-fertilizing populations of higher organisms, adaptation to the environment depends on heterozygous genotypes (Dobzhansky, 1950; Wallace and King, 1951; Wallace *et al.,* 1953; Dobzhansky and Spassky, 1953, 1954). A majority of chromosomes in natural populations of Drosophila are more or less deleterious to their carriers if present in duplicate. Yet, heterozygotes, which have two chromosomes of a pair with different gene contents, are highly fit. Natural selection appears to act by preserving in a population those chromosomes which carry gene complexes that produce fit heterozygotes with other chromosomes present in the same population.

The nature of the relationship between homeostasis and the adaptive superiority of the heterozygotes is more problematic at present. At first sight it may appear that only the average performance is of

importance for survival; that the greater the mean fecundity or the mean viability, the greater the fitness of the population. However, natural populations have become delicately adjusted to their habitats. For example, the ability to produce a large number of viable offspring under crowded conditions is of no advantage to a species if these individuals themselves show a compensating decrease in ability to reproduce. Homeostasis in regard to physiological traits similar to the ones examined here would be of importance in the evolution of a stable, well-adapted natural population of a species, by providing buffering against fortuitous environmental changes.

Perhaps even more important is the following consideration. Any organism meets during its lifetime a variety of environments; the higher organisms which are mobile and long-lived have to deal with many and diversified environments. This being the case, any genotype which is specialized to live in only one or in a narrow range of environments will probably not show high viability or high fertility in natural habitats where the environmental conditions are constantly changing. The adaptive value of a genotype is, however, determined by the average performance of its carriers in a range of environments which this genotype normally meets. Homeostasis permits the organism to compensate for environmental disturbances, and to develop and go through its life cycle despite environmental changes. If heterozygosis tends to yield superior homeostasis, heterozygous genotypes will usually be more highly fit than homozygotes with their more restricted adaptive specialization.

Summary

In laboratory populations of *Drosophila pseudoobscura* derived from the natural population at Piñon Flats and carrying Standard (ST) and Chiricahua (CH) gene arrangements, the ST/CH heterozygote exhibits an overall adaptive superiority to both homozygotes, with ST/ST, in turn, generally superior to CH/CH. The present study was designed to investigate possible sources of these differences by comparing various physiological traits which might contribute to superior adaptation. An attempt was made to raise the experimental flies under conditions resembling as much as possible those in experimental population cages.

Fecundity studies at 25° C. indicate that in total eggs per female per lifetime and in eggs per day per surviving female, ST/CH females are similar to ST/ST, and both are superior to CH/CH. At 16° C. in total eggs per female per lifetime, ST/CH females were significantly higher than CH/CH females at the .05 level of significance, with ST/ST intermediate; however, when the effect of longevity was removed, no significant differences were observed.

Longevity in the presence of food was studied at 16° C. and at 25° C. In every case, ST/CH heterozygotes lived longer on the average than homozygous flies of the corresponding sex.

A series of experiments comparing pre-adult viability were conducted at 25° C. The results indicated a decided inferiority of CH/CH in almost all cases. ST/ST, in the same environment, was at least equal to the heterozygote. However, in all of the pre-adult viability experiments, ST/CH developed more rapidly than the homozygotes.

Relative indices of general performance at 25° C. were computed. With ST/CH set arbitrarily at unity, CH/CH gave an average value of 0.443 and ST/ST an average of 1.077, as compared with adaptive values of 0.413 for CH/CH and 0.895 for ST/ST calculated from recent population cage experiments. Considering the differences in the conditions of the experiments, this agreement is as great as can be expected.

Throughout the experimental work, the variance shown by ST/CH heterozygotes tended to be lower than that exhibited by either of the homozygotes. Statistical

treatment of the combined data confirmed the reality of this trend ($p = .0005$). It can be concluded that ST/CH flies show a superior homeostatic adjustment in their development to that of either of the homozygotes. The significance of this type of homeostasis is discussed.

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CONVERGENT TRENDS IN ANOMODONTIA

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Introduction

The suborder Anomodontia is the most numerous of all the mammal-like reptiles in South Africa, not only in number of species but also in number of specimens. Many thousands of specimens are housed in collections distributed all over the world. The group was in existence for a fairly long period and lived through several climatic changes before it became extinct in the geological phase represented by the *Cynognathus* zone. The first anomodonts are found in the lower *Tapinocephalus* zone (Middle Permian) and a late form (*Kannemeyeria*) survived to the Middle Triassic. In view of the number of specimens and the relative longevity of the group, the Anomodontia present a very valuable group for the study of evolutionary problems, especially today when more and more attention is being given to the detailed stratigraphy of the Karroo, e.g., Rossouw and de Villiers' recent report on the Koup (1952). Problems such as evolutionary trends and rates, relicts and extinction can be studied very profitably. Attention will here be directed mainly to the first of these objectives, viz., evolutionary trends.

In a penetrating paper on the origin of the anomodont *Dicynodon*, Watson (1948) observes that the genus is evidently of polyphyletic origin: "the small Endothiodonts, characterised only by possessing cheek teeth in the maxilla and dentary, form a heterogenous mass, some actually 'Dicynodon' ancestors, others probably going no further." The classification of these small endothiodonts is based almost entirely on the distribution of the molar teeth on the palate and mandible (Toerien, 1953). With loss of the molar teeth in these forms, there is no way of distinguishing between their descendants. However, one *Tapinocephalus* zone genus, *Broilius*, differs in palatal structure from the other small *Tapinocephalus* zone endothiodonts, and its molarless descendants can therefore be distinguished from the otherwise very similar genus *"Oudenodon."* This latter "genus" represents the other molarless descendants of one or more small Endothiodonts.

In the genus *Dicynodon* there appear to be tusks in both sexes or in the males only whereas in *"Oudenodon"* the tusks are either absent in both sexes or present in the males only.

The further development of *Dicynodon* and its descendants can be followed with relative ease since their peculiar palatal structure, inherited from *Broilius*, remains very constant. Certain tendencies are observed.

Evolutionary Tendencies

The development of a secondary palate: In the *Tapinocephalus* zone species of *Dicynodon*, the choanae are wide anteriorly. In the later descendants the anterior parts of the choanae are reduced to slits. In some of the *Lystrosaurus* species and in *Kannemeyeria* these slits are completely closed off and reduced to sutures (Toerien, 1953).

Enlargement of the snout: The tendency for the relative increase in the size of the snout in the *Dicynodon* descendants is especially noticeable in *Lystrosaurus*. In *Daptocephalus* also, the relative increase in the snout length is marked (39% of the total skull length). In *Kannemeyeria*, the relative snout length (37%) is only slightly more than in the adult male *Dicynodon grimbeeki* (36%), and in *Aulacocephalodon* it is actually less than

in the former specimen (34%). However, the percentage given in the case of *Aulacocephalodon* is misleading since the snout is relatively very broad and massive in this specimen.

Lengthening of the pterygoid: In *Dicynodon* the anterior process of the pterygoid is widely separated from the maxillary by the transverse bone. In the four known descendants, the anterior process extends much farther anteriorly; in *Daptocephalus* its anterior tip reaches the maxillary and in *Kannemeyeria* and *Lystrosaurus* there is an extensive contact between the two bones. The transverse bone is displaced laterally in these forms, except in *Lystrosaurus* where it is apparently absent.

Development of a palatine-premaxillary contact: Characteristic of *Dicynodon* and most of its descendants is the bounding of the choanae by the palatine process of the maxillary. This process is overlapped anteriorly by the premaxillary and posteriorly by the palatine. In a *Dicynodon* species from the Endothiodon zone (*D.* cf. *ictidops*) this process is almost completely covered by the palatine and premaxillary. Another interesting specimen (No. 177 B.P.I.) comes from the middle of the *Cistecephalus* zone. It is in all respects very similar to *Daptocephalus*, but according to the definition it is still a *Dicynodon* as the pterygoids do not reach the maxillary anteriorly. On the one side of the palate there is a fairly extensive contact between the palatine and premaxillary but on the other side the two bones are separated. In *Daptocephalus* these two bones have a slight contact on both sides, and in *Aulacocephalodon* they meet extensively.

Development of bosses: Lateral bosses develop on the nasals and prefrontals in *Lystrosaurus*, *Aulacocephalodon* and to a slight degree in *Kannemeyeria*. The development of bosses probably took place independently in *Aulacocephalodon* and *Lystrosaurus* since in a primitive Lystrosaurian these bosses were very insignificant.

Lateral development of the squamosals: In *Aulacocephalodon* the squamosals develop very extensively laterally and postero-laterally.

Loss of canines: As is the case in the majority of *Dicynodon* species, all the descendants of this genus have tusks in both sexes. However, some *Dicynodon* species have lost their tusks in the females. This has certainly happened more than once. According to Boonstra (1948), *Dicynodon pseudojouberti* from the *Tapinocephalus* zone has tusks in the males only. In the much later (upper *Endothiodon* zone) *D. grimbeeki*, the tusks in the females are in the process of disappearing, so that some females are completely tuskless (Broom 1935).

The Origin of "Oudenodon"

As was shown above, it is possible that different genera of small endothiodonts gave origin to the "genus" *Oudenodon*. Watson (1948) has also drawn attention to the fact that *Tropidostoma* from the *Endothiodon* zone loses its molar teeth with old age and would then also become an *"Oudenodon."* Some later small endothiodonts (*Emydops* species) have few teeth and apparently lost them to become *Emydorhinus* and later *Cistecephalus* (Toerien, 1953). Sometimes, however, the reduction of teeth is accompanied by other changes (e.g., the broadening of the intertemporal region in *Cistecephalus*) so that these toothless forms can readily be distinguished from *"Oudenodon."* As was seen in the new *Dicynodon* specimen (No. 177 B.P.I.) mentioned above, the one side of the palate is that of an *"Oudenodon"* and only the absence of a palatine-premaxillary contact on the other side shows its *Dicynodon* affinity.

In view of the extremely probable, polyphyletic origin of *"Oudenodon,"* the presumably late tuskless descendants of this "genus," e.g., *Kitchingia*, *Platycyclops*, *Eocyclops*, *Megacyclops*, *Rachiocephalodon* and *Pelanomodon*, are, perhaps, not even closely related.

The Origin of Pelanomodon

Pelanomodon is one of the tuskless genera whose phylogeny has been very obscure hitherto. The first species of this genus (*P. moschops*) was described as a female of the genus *Aulacocephalodon;* and the absence of tusks is certainly its only significant distinguishing feature. The possibility of *Pelanomodon* being the female of *Aulacocephalodon* can, however, be ruled out since specimens of the latter genus are far more plentiful than are those of *Pelanomodon.*

Pelanomodon resembles *Aulacocephalodon* in the broad, laterally developed squamosals, large nasal and prefrontal bosses, a wide flat intertemporal and interorbital region, rather long pterygoids (longer than in *Aulacocephalodon*), a palatine-premaxillary contact and in the reduced anterior parts of the choanae (fig. 1; a, b, c and d). This remarkable similarity between the two genera might be explained by presuming that *Pelanomodon* descended from *Aulacocephalodon* through the loss of tusks. The possibility of the reversed development can be excluded. On the other hand specimens recently developed in the Bernard Price Institute for Palaeontological Research have thrown entirely new light on the origin of *Pelanomodon.*

One group of *"Oudenodon"* species to which van Hoepen (1934) gave the subgeneric name of *Mastocephalus* is characterized *i.a.* by the lack of tusks, a weak snout, and a low flat skull. Species typical of this group were *Oudenodon platyceps* and *O. kolbei.* Broom subsequently (1936) raised *Mastocephalus* to generic status. Unfortunately it is still impossible to discover criteria that adequately separate *Mastocephalus* from *"Oudenodon."*

Pelanomodon (fig. 1; c, d) differs from *Oudenodon platyceps* (fig. 1; i, j) in having relatively wide intertemporal and interorbital regions with large nasal and prefrontal bosses, large laterally developed squamosals, a long anterior pterygoid process and a relatively heavy snout (35% in *P. kitchingi* as compared to 23% in *Oudenodon platyceps*). *O. platyceps* has

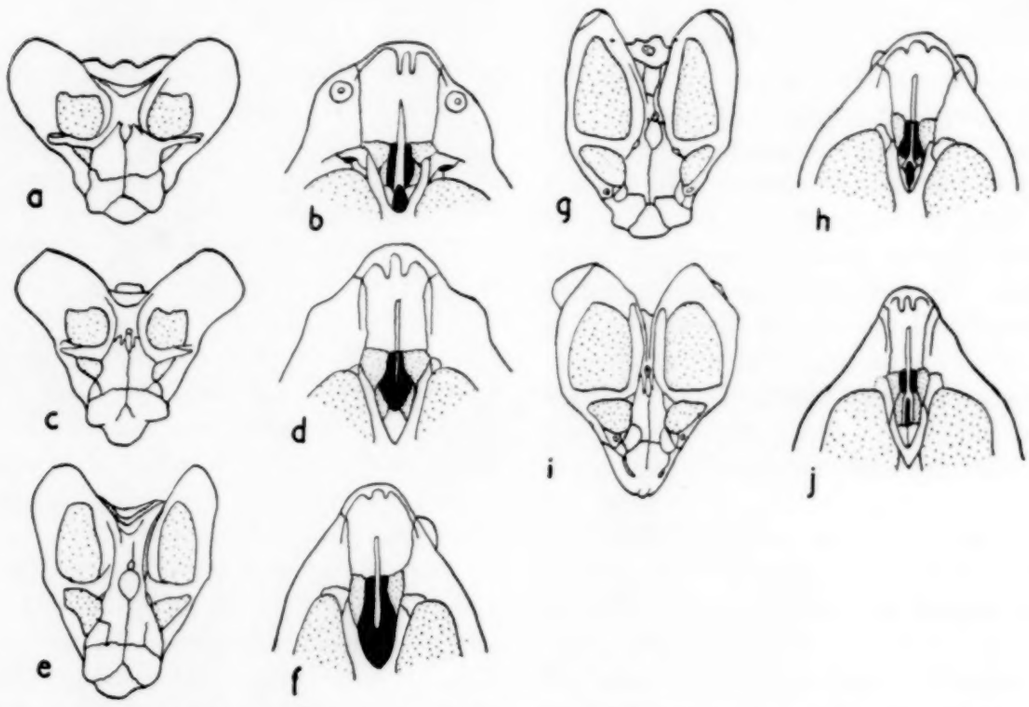

Fig. 1. Dorsal and palatal views of a) *Aulacocephalodon pricei,* b) *Aulacocephalodon vanderhorsti,* c) *Pelanomodon kitchingi,* d) *Pelanomodon rubidgei,* e and f) No. 165 B.P.I., g and h) No. 138 B.P.I., i and j) *Oudenodon platyceps,* Drawings not to scale. The palatine bone is finely stippled.

slight bosses on the nasal bones, and in an otherwise similar *Oudenodon* species in the B.P.I. Collection the bosses are more prominent. A recently developed specimen (No. 138 B.P.I.) is intermediate in structure between *Oudenodon* and *Pelanomodon*. With the latter genus, it shares the following features: The frontal region is broad, with prominent nasal bosses, and the pterygoid extends far anteriorly. The short snout (22% of total length) narrow intertemporal region and unexpanded squamosals, on the other hand, are typical of *Oudenodon* (fig. 1; g, h). A young specimen (the sutures are open) of possibly *Pelanomodon halli* (No. 165 B.P.I.) is almost identical with this other specimen except that the snout is relatively longer (30%) and the intertemporal region broader (fig. 1; e, f). These intermediate forms show conclusively that *Pelanomodon* has developed from an *Oudenodon* such as *O. platyceps*.

Discussion

Two of the trends enumerated above are common to all the known descendants of *Dicynodon:* (1) enlargement of the snout, and (2) lengthening of the anterior process of the pterygoid. These two developments are most probably related since a lengthening of the pterygoid (and its ultimate attachment to the maxillary) will strengthen the pterygoid bar for the support of the heavier snout. The secondary contact between the palatine and premaxillary in *Daptocephalus* and *Aulacocephalodon* is probably also correlated with the enlargement of the snout as it tends to strengthen the anterior part of the pterygoidal bar. A third related development is the lateral expansion of the squamosal in *Aulacocephalodon*. A larger snout would involve a larger mandible which in turn would necessitate larger muscles of mastication. The large postero-lateral expansion of the squamosals not only provides a larger surface area for the attachment of the capito-mandibularis muscle but also a stronger base for its origin. However, since the skull is very flat, opening of the snout would be very limited if the muscle fibers were in a vertical position. The postero-lateral expansion of the squamosal causes the muscle to run obliquely and the muscle fibers are therefore much longer. In *Daptocephalus* and in *Kannemeyeria* space for the expansion of the capito-mandibularis is provided for by the narrowing of the intertemporal region and its development into a crest. These four modifications in the original *Dicynodon* pattern mentioned above are most probably related to a change in diet. The significance of the bosses is more difficult to explain. It seems likely that they supported horny outgrowths or acted as bony buttresses used for attack or defence. If this view is correct, it will give an additional significance to the strengthening of the pterygoidal bars between the snout and skull base. The more extensive secondary palate was inherited from their *Dicynodon* ancester.

Pelanomodon is from the same horizon of the *Cistecephalus* zone as *Aulacocephalodon*, and presumably lived under similar environmental conditions. Selection pressure would therefore tend to produce similar modifications in both genera. However, since only the skulls are fully known, differences in the rest of the skeleton may be found in future.

Classification of Trends

The complete absence of teeth in *Cistecephalus* and some species of *"Oudenodon,"* which developed from small toothed endothiodonts, and the independent development of bosses in *Aulacocephalodon* and *Lystrosaurus* can be regarded as cases of parallel evolution since the genera can still be very easily separated (Haas and Simpson, 1946).

The loss of molars in the descendants of *Broilius* and the *"Oudenodon"* ancestors reduces the number of distinguishing features between *Dicynodon* and *"Oudenodon,"* and must therefore be regarded as an example of convergent evo-

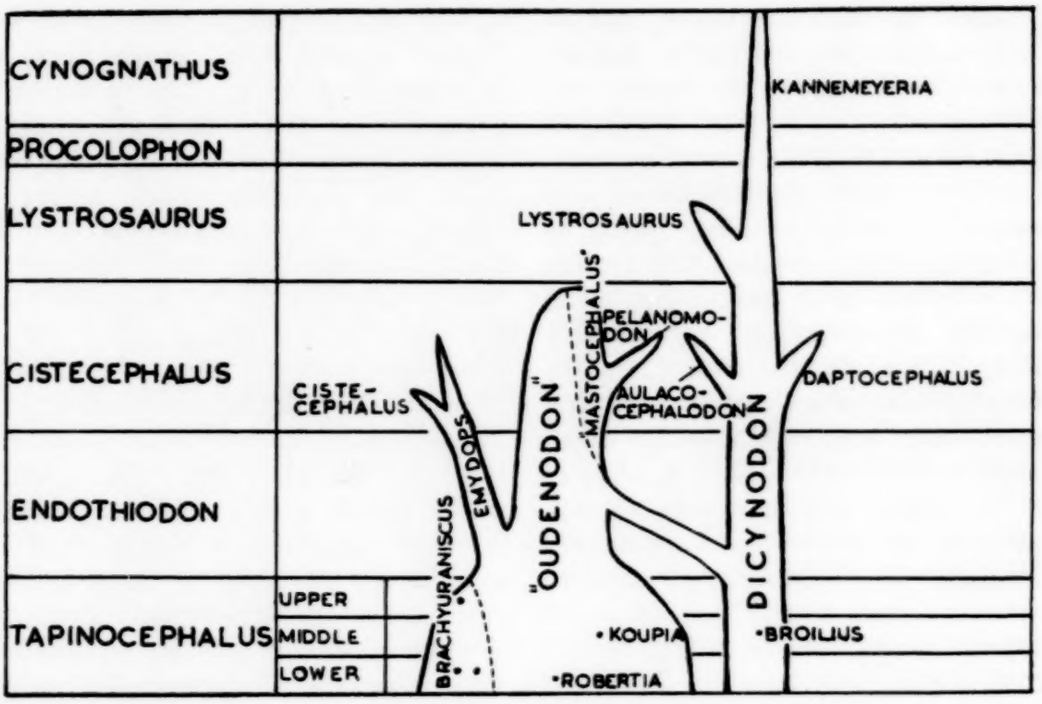

FIG. 2. Graphic representation of the polyphyletic origin of *"Oudenodon"* from the small Endothiodonts and *Dicynodon*, and the distribution in time of some important Anomodontia.

lution. So great is that convergence that the differences between the genera *Dicynodon* and *"Oudenodon"* are concealed to the point where the one can be mistaken for the other. Their development can consequently be regarded as a case of homoeomorphy (Haas and Simpson, 1946).

The extremely likely polyphyletic origin of *"Oudenodon"* from several small endothiodonts and from *Dicynodon* (represented graphically in figure 2), and the remarkable development of similarities between *Pelanomodon* and *Aulacocephalodon* represent extreme cases of homoeomorphy. The loss of canines in the females of *Dicynodon* at different stratigraphic levels may be regarded as an example of iteration, but since there is very little difference between these "offshoots" it can also be regarded as a case of heterochronous homoeomorphy.

I wish to extend my sincere thanks to Professor R. A. Dart, Head of the Department of Anatomy and to Dr. A. S. Brink and Mr. J. W. Kitching of the Bernard Price Institute for Palaeontological Research for their help in this investigation.

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THE EVOLUTION OF NEST-BUILDING BEHAVIOR IN *APICOTERMES* (ISOPTERA) [1]

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INTRODUCTION

The relative non-existence of ethological fossils (with such exceptions as fossil tracks and burrows) and the transitory nature of movements and behavior patterns makes the study of the evolution of behavior extremely difficult. It is not surprising that the number of papers dealing with this subject is so small compared to the vast literature on the evolution of morphological structure.

The nests of the African genus of termites, *Apicotermes,* present unique material for the study of the evolution of behavior. These species-specific structures are tangible products of the nest-building behavior of the entire colony, and permit an ethological study of a supraorganism in contrast to an organism. They are relatively permanent and may be studied in the laboratory at leisure. The known nests present an unusually complete phylogenetic series, and it can be expected that this series will be considerably improved as future collections fill in existing gaps. In this genus, the nests show phylogenetic relationships much more clearly than do the morphological characteristics of their builders. Emerson (1938) summarizes the attributes of termite nests as follows:

"Termite nests may be used as examples of behavior evolution because they are morphological indications of behavior patterns, they express the behavior of a population, the patterns are hereditary, there is a natural control over any Lamarckian influence, evolutionary sequences are available, adaptive modifications may be demonstrated, and coordination mechanisms may be partially analyzed."

Of the many types of structures (nests, webs, cases, etc.) produced by various organisms, the nests of termites present one of the best materials for the study of the evolution of behavior, and the nests of *Apicotermes* are far superior in certain respects to the nests of other termites. In *Apicotermes,* the nest of each species is unusually characteristic of that species in contrast to the nests of many of the other termites which often vary conspicuously only between genera. Such a complete phylogenetic series of so many species within a single genus is also rare among termites.

This type of study will probably be criticized by some, who will point out that a description of the nest does not describe the actions or processes performed in building the nest. This cannot be denied. However, it must be emphasized that this paper deals not with a *description* of the nest-building behavior but with the *evolution* of this behavior. There can be little doubt that the nests of *Apicotermes* are valid indicators of the phylogenetic relationships of the behavior producing them.

The known nests of *Apicotermes* have been described in detail by Desneux (1918, 1948, and 1953) and the termites themselves by Emerson (1953). Both of these workers have discussed the phylogeny of the genus (Emerson, 1952a, 1953 and Desneux, 1948, 1953). This paper, leaning heavily upon the work of these two men, will attempt to deal with the phylogeny of the genus in greater detail, using additional data as well as oc-

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casional reinterpretation of some previous data. Certain aspects of the evolution of these nests will then be discussed.

Methods

Sources and Types of Material

Measurements were taken from three sources. The only nests available for study were some fragments in the custody of Dr. A. E. Emerson at the University of Chicago. These nests were received from the Musée Royal du Congo Belge, T. E. Snyder, Professor P.-P. Grassé, and Dr. J. Desneux. This collection was especially useful in that it provided the most accurate set of measurements made. Extensive use was made of photographs in the 1948 and especially the 1953 papers of Dr. J. Desneux. Radiographs were made of the nest walls of the specimens in Emerson's collection.

Radiographs of Nest Walls

Radiographs were obtained by merely laying the nest fragment on a piece of film and irradiating from above. The film was kept small to reduce errors resulting from the curvature of the nest. The nest and film were exposed at about one meter from the target in order to reduce errors due to divergence of rays. Kodak Super Ortho-Press was wrapped in black paper and used as film. The results were reasonably satisfactory, although use of better materials and techniques might possibly have given somewhat better resolution of certain wall structures. The best resolution was obtained at about 30–50 kv., depending upon the nest fragment used. A few of the more interesting radiographs are shown in figure 5.

Methods of Measuring

The size and accessibility of the structure determined the method by which it was measured. Nest structures smaller than 1 cm. were generally measured by an ocular micrometer in a dissecting microscope. Measurements of less than 1 cm. from photographs were usually made with fine-pointed calipers, the distance between the points of the calipers being determined by placing them against an ocular micrometer with a 1 cm. scale. Measurements greater than 1 cm. were made with calipers and a metal rule calibrated in millimeters. Areas were measured with a planimeter. In a few cases the area was too small to be measured directly by this method. The area was then enlarged with a microscope and camera lucida and the enlarged area determined with a planimeter.

Accuracy of Measurements

A number of sources of error are inherent to the methods used in this study. An extensively used character is the length of the internal slit. These are internal openings of conduits that pass through the nest wall. Errors in the measurement of these slits result from the difficulty in actually defining the structure. Slits are often closed to varying degrees with sand or mortar, making it very difficult to determine the exact limits of the structures. Because of this, different observers might obtain slightly different measurements due to different concepts of slit limits. However, several checks used indicate that the measurements of these structures are somewhat more accurate than one would suspect from the difficulty just mentioned. Slits measured from radiographs (fig. 5) gave results similar to those obtained directly from the nest. Measurements of a small number of slits, the conduits of which had been sectioned horizontally (fig. 3) also provided a good check. Such horizontal sections through the conduits exposed the slit free from obstructing material, thus providing the most accurate measurement of this structure. Although this is the obvious solution to the difficulty of slit measurement, it is not practicable at present. This method would require the almost complete destruction of the portion of nest being used, which would, of course, be inadvisable with such rare material.

The use of photographs of curved structures also introduces errors that are difficult to avoid. So far as possible, only those portions of a photograph were used in which the object photographed was in focus and in a plane parallel to the plane of the film. Even so, much of the variability of data from photographs is undoubtedly due to such factors as curvature.

It would be expected that the distance between centers of external parietal openings would be slightly greater than the distance between the centers of the corresponding internal parietal openings of the same nest because of the radial arrangement of these structures. It will be noted in table 1 that this is not always the case. This is because the two sets of measurements were often made from different photographs or nest fragments.

Some of the larger samples of measurements of the length of the internal slit, interval between slits, and distance between centers of external pores were checked to see if they fitted the normal curve. It was found that they fitted reasonably well.

Choice and Arrangement of Data

Both the vertical and horizontal curvature of the nest vary along its vertical axis. This usually results in the wall structures of the two poles being somewhat different from the rest of the nest. Since the poles were generally not available for study, measurements have been restricted to the equatorial, central portions of the nest wall. It also seemed advisable to exclude portions obviously modified by such factors as the presence of an adjacent ramp or a root passing through the wall. Only the most accurate data obtained have been presented in table 1. Data have been excluded for which the accuracy was for some reason questionable (e.g., due to excessive curvature or unknown magnification in the case of a published photograph). When sufficient data have been available directly from a nest fragment, these have been given preference over data obtained from photographs.

Table 1 has been arranged according to locality and species. Since the variability within species has not received adequate taxonomic evaluation, it did not seem advisable to lump all data for a single "species." Therefore local populations, in many cases probably single colonies, have been dealt with separately.

Highly accurate nest measurements and large samples will not be possible until nests may be spared for dissection and more extensive collections are available.

General Nest Characteristics and Terminology

Apicotermes belongs to the Termitidae, the most advanced family of termites and is one of the more primitive genera in the subfamily Termitinae (Ahmad, 1950). Most of the closely related genera are subterranean, but unfortunately their nests are unknown. Eventual collection of their nests should add much important information about the origin of *Apicotermes.*

Only sufficient description of nests need be given here to permit discussion of nest phylogeny. The reader is referred to the papers by Desneux (especially his 1953 paper) for detailed description and photographs.

The shape of the nest varies with the species, but is more or less oval, somewhat similar to an American football. The height varies from about 4 to 42 centimeters. These subterranean nests are usually found in sandy soil in rainforests, although two species with known nests inhabit savanna. Nests have been found at depths up to 60 centimeters. A single colony probably consists of several nests connected by tunnels.

The external surface of the nest shows a porous covering composed of grains of sand and having the appearance of foam rubber. Desneux calls this the shagreen

Species and Locality	Length of Internal Slit Mean±S.E. (No.)	Distance between Internal Slits Mean±S.E. (No.)	Distance between centers of Slits	Distance between Centers of External Pores Mean±S.E. (No.)	Conduit Width ext./center/ int.	Unenclosed Area/ Total Area	Story Height	Lamella Thickness
A. lamani								
Luki	2.94±.04 (116)	4.31±.16 (90)	7.24				8.3	
? loc.	2.89±.05 (53)	4.41±.18 (49)	7.30				9.7	
Zobe			7.00				9.1	0.6
Weka-Kaï Dunda							7.2	0.6
Bas Congo							10.0	
A. arquieri								
Bossembele				6.11±.24 (31)			10.0	1.5
A. "occultus"								
Konakry							9.5	1.0
Bas Congo								
Landana	5.46±.25 (19)	3.23±.17 (17)	8.69	8.79±.39 (8)			7.6	0.5
Weka-Kaï Dunda	5.13±.16 (36)	2.90±.17 (29)	8.03	9.19±.28 (29)			6.7	0.5
Mayumbe								
Bucco Zao	3.61±.11 (9)	4.31±.53 (7)	7.92	10.78±.14(156)	1 /1 /1		7.1	0.5
Chibuete				11.27±.65 (9)			8.3	
A. gurgulifex								
Mayidi			9.50	8.20±.17(82)		0.39	6.2	0.5
? loc.	2.80±.07 (14)	6.63±.96 (10)	9.43	10.11±1.05 (10)	.9/ .9/1		7.5	
A. deneuxi								
Bamba Kilenda	3.48±.14 (24)	3.57±.23 (24)	7.05	7.15±.09 (68)	1.0/1.0/1	0.23	7.0	0.5
Unknown sp.								
Mayidi				8.03±.18 (23)		0.10	6.3	
A. kisantuensis								
Kondue (I)	2.73±.09 (15)	3.23±.19 (13)	5.96		1.9/1.1/1		5.9	
Kisantu (I)					1.7/1.1/1		7.0	
Boende (I)	3.88±.05(87)	3.48±.09(78)	7.35	7.51±.16 (39)	1.4/ .9/1		7.2	
Kole (II)	2.45±.07 (12)	4.25±.15 (9)	6.70		1.1/ .4/1			
Mayidi (II)	3.33±.03(207)	3.06±.05 (190)	6.39	5.93±.24 (27)	1.0/ .6/1		6.6	0.6
A. angustatus								
Bamba Kilenda (A)	2.96±.05 (35)	3.91±.27 (26)	6.87	7.57±.29 (14)	.6/ .3/1		7.2	0.5
Kondue (B)				7.24±.06(285)	.4/ .2/1	0.04	7.2	0.7
Lodja (B)	2.91±.04 (75)	3.24±.10 (57)	6.15	6.60±.16 (45)			6.6	0.6
A. porifex								
Luluabourg			5.66	6.80±.29 (14)	.2/ .1/1		6.5	
Kipala			5.88	7.06±.35 (17)			6.3	0.6

TABLE 1. *A Comparison of Nest Measurements from Different Species and Localities*

network. Several types of this network are found.

Excrement, saliva, and extraneous material such as sand, dirt, and wood particles are used by various termites in their constructions (Emerson, 1938). The bulk of the nest material in *Apicotermes* is composed of excrement (Grassé and Noirot, 1948b) although the shagreen network seems to be built largely of grains of sand.

A vertical section through the nest shows it to consist of a number of horizontal, parallel stories separated by thin lamellae (fig. 1). Each lamella is from 0.5 to 1.5 mm. thick, depending upon the

species. The distance between the centers of adjacent lamellae is from 6 to 10 millimeters.

Communication between the different floors is made possible by ramps. These are of two types—direct and helicoidal (Desneux, 1953). The former permits a more or less direct course by termites moving between floors, while the latter imposes a spiral course, necessitating an alternation from one side of the ramp to the other as the termite moves along.

The most characteristic feature of this genus is seen in the various systems of perforation of the nest wall, permitting the exchange of gases between the interior and exterior of the nest. Only one species lacks such a system, having lost it secondarily. The particular type of perforation is characteristic of the species (figs. 1, 2, and 5). In most species internal parietal openings are found which are small, discrete, horizontal slits. These average between 2.5 and 5.5 mm. in length, depending upon the species. These slits are the internal openings of conduits that run directly to the outside through projections, pass into long funnels, or open into circular galleries. The circular gallery is a horizontal tube enclosed within the nest wall and continuous around the entire circumference of the nest. The small size of the internal parietal openings prohibit their use as passages into the galleries or to the outside of the nest. With the exception of the nests of *A. "occultus,"* the circular galleries open to the exterior through small external pores.

In those nests with discrete internal slits the portion of the wall between slits usually protrudes slightly toward the center of the nest to form a pilaster.

In some nests, the conduits are lined with a special material differing in composition from the rest of the nest.

A Phylogeny of Nests

The phylogeny given here is based largely on nest structures. Only two species of *Apicotermes, A. trägårdi* and a new species from Nyasaland, are without known nests. On the other hand, a number of nests have been described for which no inhabitants have as yet been collected. These are usually referred to

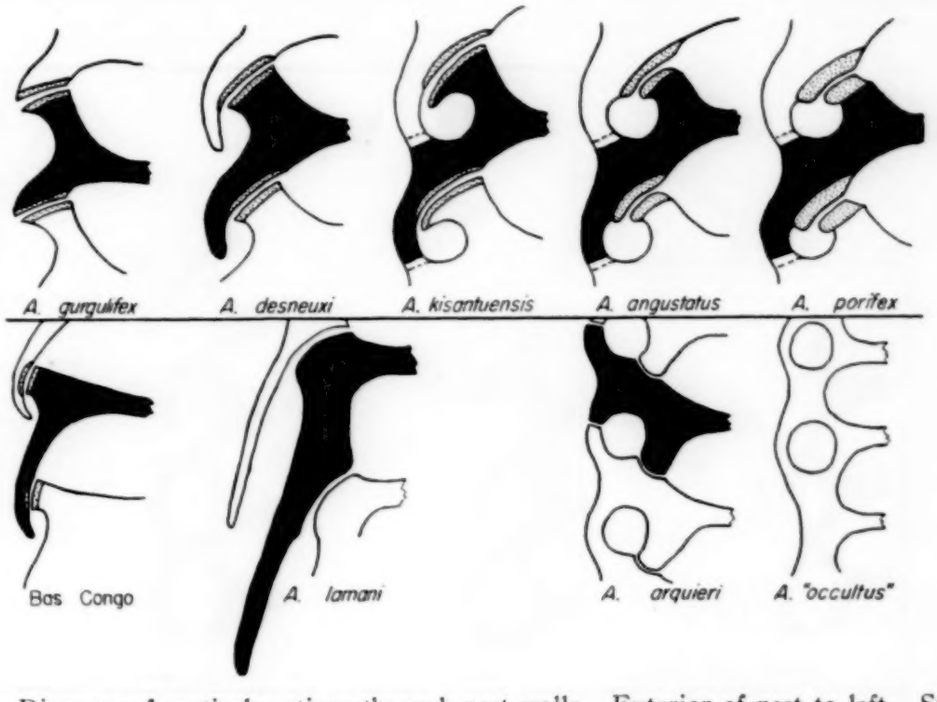

Fig. 1. Diagram of vertical sections through nest walls. Exterior of nest to left. Stippling indicates lining material. Black indicates a lamella plus attached wall structures. (Compiled and modified from Desneux, 1948 and 1953.)

by the name of the locality from which the nest was first discovered. A key to nests, based on the phylogeny of the genus as given here, is included to emphasize phylogenetic relationships. The phylogeny may be most conveniently discussed by dividing the genus into three groups: the *"occultus"* group (left branch of figure 4) the *porifex* group (right branch of figure 4 exclusive of the Bas Congo nest), and the Bas Congo nest.

The *"occultus"* Group

This is a group of three species indicated on the left side of figure 4. These show a number of distinct differences from the remaining members of the genus. Unfortunately, as complete a phylogenetic series is not available here as in the *porifex* group. At present it is not possible to say whether this is due to extinction of the intervening species or to failure, as yet, to collect these species.

The *A. "occultus"* nests are only assumed to belong to that species on the basis of locality, the termites never having been collected together with the nest.

The nests of this group are found in the soil surrounded by a space (the orientation of *A. "occultus"* has not yet been observed). This is in contrast to species of the other groups whose nests are surrounded by an envelope of sand.

The shagreen network is another character distinguishing the *"occultus"* group. Here the shagreen layer is a much more intimate part of the wall than in other nests, and will not chip off cleanly. This layer forms a uniform covering of the external surface of the nest.

The distance between floors is generally greater than in other groups (table 1).

The internal parietal openings of this group (when they occur) pierce the wall near the bottom of a story, i.e., less than half-way from the floor to the ceiling (fig. 1).

The distinctness of this group is further verified by the taxonomic studies of Emerson (1953). He finds that the postmentum of both *A. lamani* and *A. arquieri* is constricted at the center, while the postmentum of members of the *porifex* group has parallel sides. The species name *A. arquieri* is based upon data furnished by Pierre-P. Grassé and Charles Noirot and should be ascribed to these authors.

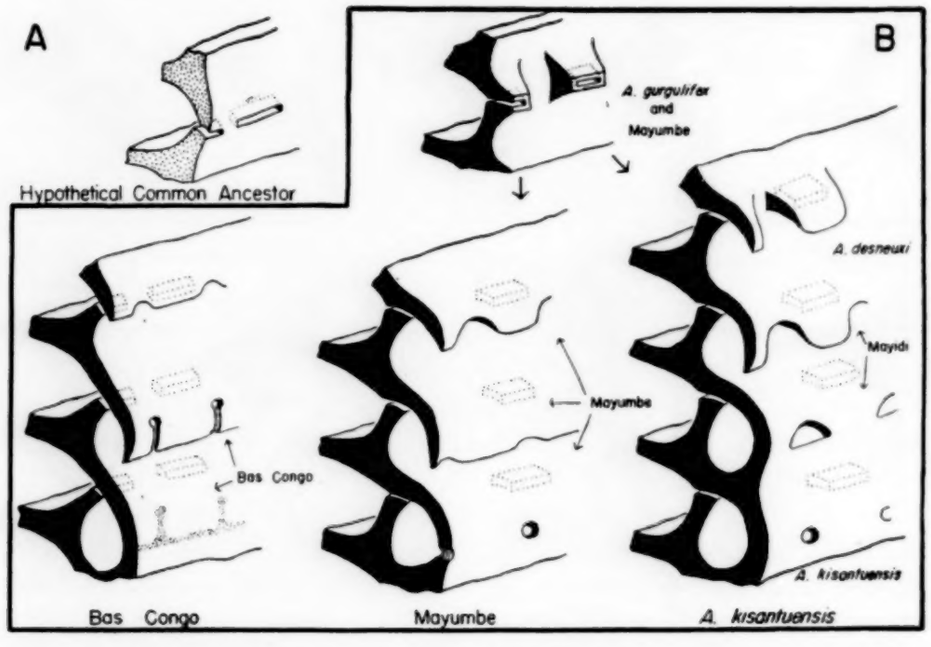

FIG. 2. *A.* Hypothetical common ancestor of known nests. *B.* A few stages of hypothetical gallery ontogenies suggesting a recapitulation of certain phylogenetic stages. Labeled stages are found in known nests.

The *"occultus"* group is subdivided by a number of distinct features. *A. arquieri* and *A. "occultus"* are closely related as shown by the ramps of their nests. In all other nests the ramps are direct, i.e., the termites can pass along them in a more or less direct course. However, here the ramps are helicoidal, requiring a twisting course by the termite using them. The unique helicoidal ramps of this pair are concentrated largely in the central axis of the nest, in contrast to the more scattered arrangement of the direct ramps in other species.

As indicated in table 1, *A. arquieri* and *A. "occultus"* are the only species studied with floor thicknesses as great or greater than 1 millimeter.

Circular galleries are present in both *A. arquieri* and *A. "occultus"* nests. In the latter species the galleries are completely isolated, their internal and external openings apparently having been lost through regressive evolution (fig. 1). These galleries often end blindly, rather than continuing around the entire circumference of the nest.

The conduit from the internal parietal opening to the gallery is continuous throughout the entire circumference in the nests of *A. arquieri*. The conduits of all other species consist of discrete, separate units (fig. 5). These continuous conduits probably arose phylogenetically through the lateral fusion of discrete conduits. This probably took place after the origin of galleries, because of the lack of wall support given by continuous conduits alone. Desneux (1953) also notes that pilasters are found in some of the lower portions of *A. arquieri* nests. These are apparently similar to the pilasters found between discrete slits, except that here the internal slit continues past the distal side of the pilaster.

As noted by Desneux (1953), the relation of the wall structures in *A. arquieri* is radically different from that of other nests with circular galleries (fig. 1). The gallery is opposite the *ceiling* of the story from which its internal slit originates. In other species the gallery is opposite the *floor* of the story from which the internal slit opens. This difference is also shown by comparison, between different species, of a lamella plus attached wall structures. It is seen that in the *porifex* group the galleries are formed by a *downward* projection of the upper lip of the external openings of the conduits. In *A. arquieri* this part of the wall structure sweeps *upward*.

A. arquieri is the only known species showing meridional galleries, running vertically within the nest wall (fig. 5).

In the nests of *A. lamani*, discrete internal parietal slits open to the exterior through long funnels (figs. 1 and 5), and the ramps are direct and scattered. These characteristics distinctly separate this species from the other two members of this group. The presence of internal slits and direct ramps suggests that *A. lamani* is primitive, having arisen soon after the divergence of the *"occultus"* and *porifex* groups. The interval between slits considerably exceeds the length of the slits (table 1).

Desneux (1948, 1953) shows a nest (from Zobe) similar to *A. lamani* in all respects except for the internal parietal openings. These are pores in this particular nest, rather than slits. Desneux suggests that this difference may be the result of weathering of the nest fragment, part of the lining material around the slits having been eroded away, leaving only pores. Table 1 shows that the few measurements that could be made from this photograph fairly closely correspond to other *A. lamani* specimens.

The position of *A. lamani* given here differs only slightly from that of Desneux's (1953) phylogeny. He derives this nest from the base of the *porifex* group because of the direct ramps and discrete slits.

Two other termites (without known nests), *A. trägårdhi* and a new species from Nyasaland, share with the *"occultus"* group the characteristic of a constricted postmentum (Emerson, 1953 and

personal communication). These species would probably fall somewhere below *A. lamani* in the phylogeny presented here. Emerson (1953) considers *A. trägårdhi* to be the most primitive of the known species of *Apicotermes*.

The *porifex* Group

This group is composed of a remarkably complete phylogenetic series as shown by the evolution of the circular galleries and the gradual modification of the conduits. Emerson (1953) shows, from the study of the termites, that the members of this group are closely related, but states that their morphological characteristics do not permit one to be certain of their phylogenetic order. This order is much more clearly shown by the nests.

All nests of this group that have been observed in their natural relation to the soil have been found to be surrounded by an envelope of sand, rather than by a space as in the preceeding group. The shagreen network resembles in many ways that of the *"occultus"* group, but differs in two important respects. Instead of being tightly bound to the nest wall, it is very loosely applied and may be easily chipped away, making a clean, abrupt break with the nest wall. This network is thinly scattered over the external surface, rather than forming a uniform covering.

The internal parietal openings generally pierce the wall higher than half-way from the floor to the ceiling (fig. 1). The ramps are always direct and scattered. The distance between the centers of adjacent lamellae is less than in the *"occultus"* group and the floor thickness is less than in the *arquieri-"occultus"* pair.

The *porifex* group is characterized by discrete internal parietal openings, whose length varies from about 2.7 mm. to 3.9 mm. (table 1), averaging about 3 millimeters. The postmenta of all members of this group that have been studied have parallel sides (Emerson 1953 and personal communication).

A. gurgulifex to *A. porifex* series: The evolution of circular galleries can be seen in the series beginning with *A. gurgulifex* and ending with *A. kisantuensis* (figs. 1 and 2). The species name *A. gurgulifex* is based upon data furnished by Alfred E. Emerson and should be ascribed to this author. The nest of *A. gurgulifex* has been described by Desneux and was previously referred to as the nest from Kisantu due to the absence of known inhabitants prior to a recent discovery of associated termites. In the nests of this species, the wall is perforated directly by horizontal conduits beginning with internal parietal slits and opening to the exterior through projections called gargoyles by Desneux. The nest of *A. desneuxi* shows a beginning of gallery development. This nest is similar to that of *A. gurgulifex*, with the exception of the downward projection of the upper lip of the external opening of the conduit to form a hood. The distal ends of these hoods approach but do not fuse with the nest wall. Although the nests of *A. gurgulifex* and *A. desneuxi* differ considerably, the soldier termites differ only slightly in structure (Emerson, personal communication). A nest from Mayidi, for which the termites are unknown may illustrate the next step in the evolution of circular galleries. Here the distal ends of the hoods often fuse with the wall of the nest forming, at places, galleries completely enclosed except for openings that remain between the hoods. The circular gallery is finally completed in the nests of *A. kisantuensis*, becoming entirely enclosed except for small external pores. The species following *A. kisantuensis* in this group, *A. angustatus* and *A. porifex*, also have complete circular galleries.

Table 1 gives a rough measurement of this progressive closing-in of the galleries. These figures were obtained by dividing the area of the outside of the nest (below the internal slits and not enclosed by projecting upper lips of the external conduit openings) by the total area. The figure thus obtained gradually

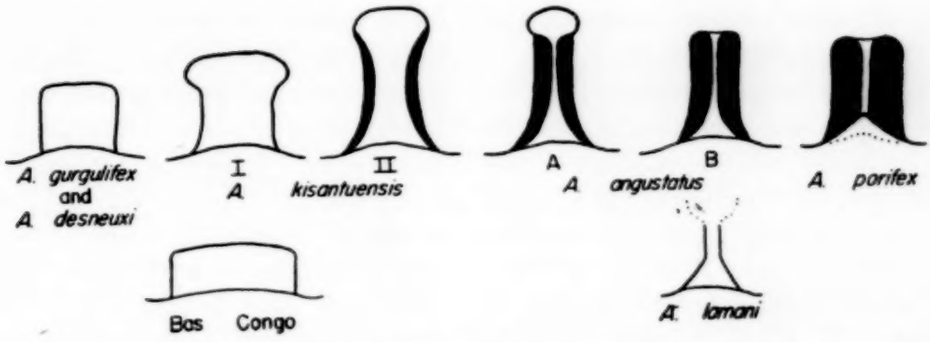

FIG. 3. Diagram of horizontal sections through discrete conduits. Internal opening at the bottom. Black indicates lining material. (Mostly modified from Desneux, 1953.)

decreases as the amount of unenclosed area decreases.

The progressive enclosure of the galleries in this series as well as the fact that the nest from Mayidi shows several stages of enclosure within the same nest, suggests strongly that the phylogeny of galleries may closely parallel the ontogeny of galleries in a single nest. Figure 2 illustrates a hypothetical method of gallery construction. Unfortunately the actual process has not been observed. However, a method of gallery formation such as illustrated would certainly be the simplest and has proved to be of great value in the study of the phylogenetic order of nests. The evolution of the galleries in this series can best be visualized by studying figure 2.

Desneux (1953) points out the phylogenetic significance of conduit changes through the series from *A. kisantuensis* to *A. porifex* (fig. 3). In the nest of *A. gurgulifex* the sides of the conduit are straight and its internal and external openings about equal in width. As nearly as can be determined from a single photograph in Desneux (1953), the conduits of *A. desneuxi* are about the same as those of *A. gurgulifex*. Two types of nest, as characterized by different conduits, have been included under *A. kisantuensis*. The conduits of the first type, *A. kisantuensis* I, differ from the previous nests by the projection of large tooth-like structures from their floors into the circular galleries (figs. 1 and 5), the sides of each conduit remaining parallel. This tooth is homologous to the lower part of the gargoyles of *A. gurgulifex*. The conduits of *A. kisantuensis* II differ further by a constriction of their sides at the center. *A. angustatus* also consists of two main types. *A. angustatus* A differs from *A. kisantuensis* II largely by the increased constriction of the lumen of the conduit. The teeth projecting into the galleries are also reduced. These teeth entirely disappear in *A. angustatus* B. Here the entrance of the conduit into the gallery may be almost level with the gallery wall or may take the shape of a slightly raised, tube-like projection (figs. 1 and 5). In both types of *A. kisantuensis* the width of the conduit at its center is about one-half or more of the proximal width (i.e., the width of the internal slit), while both types of *A. angustatus* have conduits with central widths about one-fourth or less of the proximal width (table 1). The conduit is further constricted over most of its length in the nests of *A. porifex*, and the internal opening is no longer a slit but a pore. The opening of the conduit into the gallery is similar to that of *A. angustatus* B. The increased narrowing of the lumen of the conduit in this series is paralleled by an increase in the amount of special lining material of the conduit (figs. 1 and 3).

The *A. porifex* nest from Kipala apparently differs from the Luluabourg specimen only by the absence of this lining material. This may merely be the result of erosion of the nest fragment before discovery (Desneux, 1953). The

differences between measurements of the two nests is only slight (table 1).

Table 1 gives measurements that illustrate the changes of the conduit in this series. The width of the conduit floors of different species was measured at each end and at the center. The average for each measurement was then divided by the mean width of the internal opening of the conduit. A 1 : 1 : 1 ratio is seen until *A. kisantuensis* is reached. The first figure then greatly increases because of the wide tooth projecting into the gallery. In *A. kisantuensis* II, the second figure is reduced by about one-half as the conduit narrows at the center. The rest of the series is characterized by a continuing smaller ratio as the lumen of the conduit narrows farther and the tooth disappears.

The number of internal slits per unit length seems to be somewhat greater in nests of *A. kisantuensis* and following species than in *A. gurgulifex, A. desneuxi,* or the nest from Mayidi. This is indicated by a decrease in the distance between centers of slits and the distance between external pores (table 1).

Variation in *A. kisantuensis* and *A angustatus:* Desneux (1948, 1953) has suggested that the various nests now grouped under *A. kisantuensis* and *A. angustatus* may actually represent more than just two species. It is likely that when sufficient material (both termites and nests) becomes available, splitting of these species may be necessary. The two types of *A. kisantuensis* (I and II) and of *A. angustatus* (A and B) may each represent at least a single species or subspecies.

Especially in *A. kisantuensis,* there seems to be considerable variation between different populations. Many of these differences are significant. The nest from Boende in particular seems to differ from other *A. kisantuensis* nests (table 1). The width of the internal slits, the distance between the centers of the slits, the distance between centers of

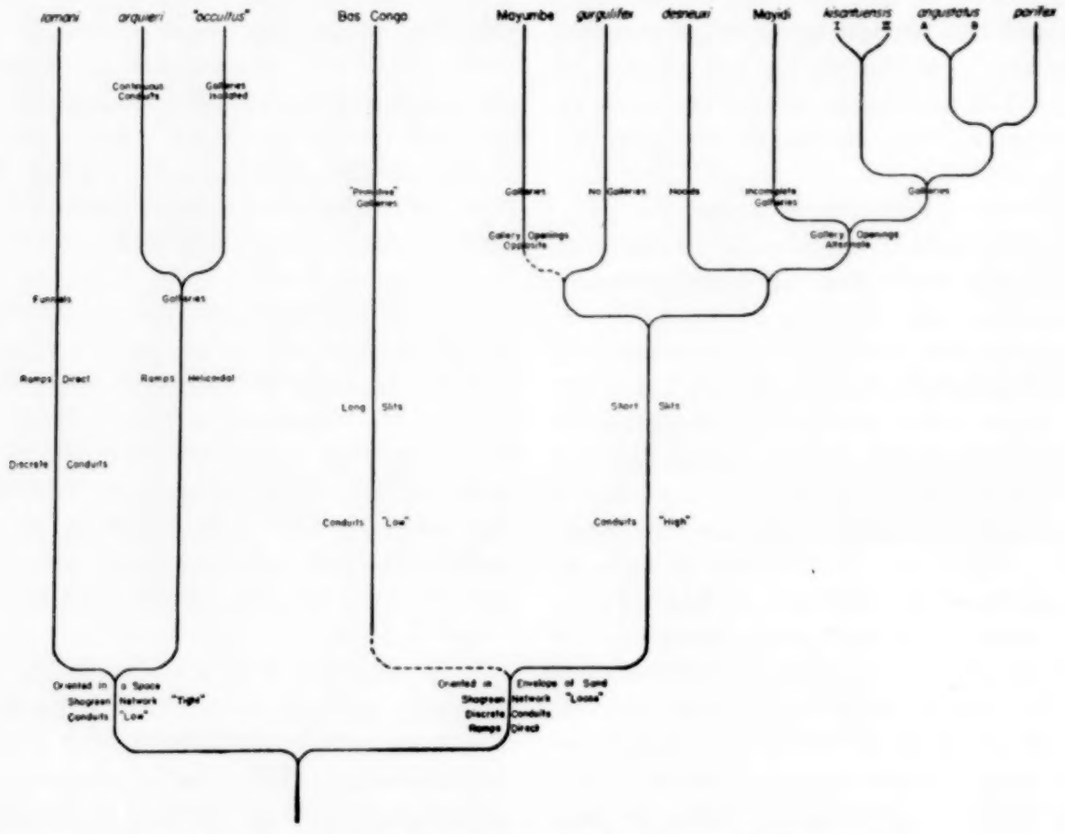

FIG. 4. A hypothetical phylogeny of *Apicotermes* based on nests.

KEY TO NESTS OF APICOTERMES

A. Oriented in a space. Discrete internal slits absent, or if present opening into funnels. Shagreen network adhering closely to surface. Ramps helicoidal except in *A. lamani.*
  B. Internal slits opening into funnels. Ramps direct.....*A. lamani*
  BB. Circular galleries present. Ramps helicoidal.
    C. Conduits continuous. .....*A. arquieri*
    CC. Galleries with neither internal nor external openings.....*A. "occultus"*
AA. Oriented in envelope of sand. With discrete internal openings. Shagreen network loosely applied and easily broken off. Ramps direct.
  B. Internal slits long (mean greater than 4.5 mm.) and less than half-way from floor to ceiling. Heavy shagreen network uniformly covering external surface.....Bas Congo
  BB. Internal slits short (mean less than 4.5 mm.) and more than half-way from floor to ceiling. Light shagreen network scattered over external surface.
    C. Galleries absent. No overhanging of upper lips of external conduit openings. .....*A. gurgulifex*
    CC. Galleries complete, or partially enclosed by overhanging upper lips of external conduit openings.
      D. External and internal openings of galleries opposite.....*Mayumbe*
      DD. External and internal openings of galleries, when complete, alternate.
        E. Galleries not in complete form.
          F. Upper lip of external conduit opening projecting downward but not quite reaching wall at distal end. .....*A. desneuxi*
          FF. Projecting upper lip of external conduit opening often fusing with wall at distal end. .....*Mayidi*
        EE. Gallery in complete form.
          F. Opening of conduit into gallery forms a large tooth. Width of conduit at center about ½ or more of width of internal slit.
            G. Tooth large. Sides of conduit more or less parallel.....*A. kisantuensis* I
            GG. Tooth smaller. Conduit narrowing at the center.....*A. kisantuensis* II
          FF. Opening of conduit into gallery in form of small tube or very slight tooth, or not raised at all. Width of conduit at center about ¼ or less of width of internal conduit opening.
            G. Internal opening a slit.
              H. Opening of conduit into gallery forming a small tooth. *A. angustatus* A
              HH. Opening of conduit into gallery smooth or forming slight tube. .....*A. angustatus* B
            GG. Internal opening a pore. .....*A. porifex*

adjacent lamellae, and the diameter of the circular galleries are greater than in other nests of this "species."

The external surface of the nests of *A. kisantuensis* and *A. angustatus* also shows considerable variation. The external pores may protrude very little from the nest wall or may open through projections of various sizes and shapes. Enough material was not available to study this character.

To what extent the variability found within species and major nest types of *A. kisantuensis* and *A. angustatus* represents specific, racial, or environmentally produced differences cannot be determined at present.

The nest from Mayumbe: This nest is of special interest since it seems to show different stages of gallery formation within the same specimen. Complete circular galleries are present in the greater portion of the nest. However, a few of the lower stories show only simple conduits and gargoyles as in the nest of *A. gurgulifex*. Between these two zones, there exists a row or two of gargoyles in the process of lateral fusion and extension of the upper lip of the external opening. This nest has led Desneux (1948, 1953) to postulate construction of the galleries for this nest as illustrated in figure 2. There is no reason to suppose that this process is essentially different for other

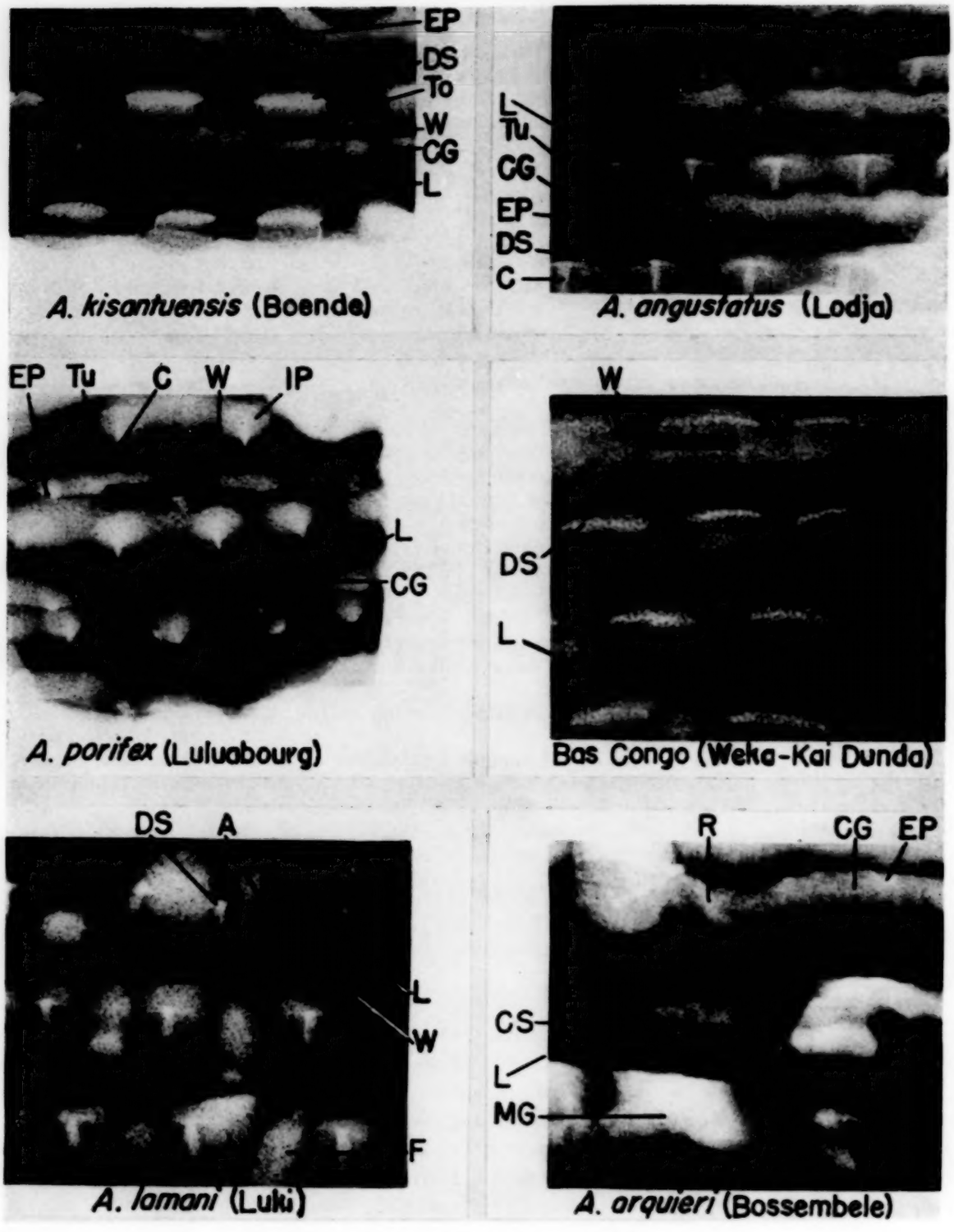

FIG. 5. Radiographs of nest walls (2×).

L—lamella
DS—discrete internal slit
EP—external pore
C—conduit
To—tooth projecting into gallery
Tu—tube projecting into gallery
IP—internal pore
CG—circular gallery
F—funnel to exterior
A—anastomosis of two funnels
CS—continuous internal slit
MG—meridional gallery
R—root enclosed in nest wall
W—wire glued to nest for purpose of orientation

members of the *porifex* group possessing galleries or for the nest from Bas Congo.

Due to the many similarities, one might suppose that the nest from Mayumbe belongs to the *A. gurgulifex-A. porifex* series. However, Desneux (1948, 1953) points out a basic difference that makes it impossible to consider this nest closely related to the other members of the *porifex* group with galleries. The hypothetical ontogeny of the circular galleries, although superficially similar to that of *A. kisantuensis,* can be seen to be different (fig. 2). The construction of galleries in these two branches of the *porifex* group seems to be analogous and therefore convergent, rather than homologous. In the development of galleries in *A. kisantuensis* the external pores are openings left *between* the downward projecting upper lips of the gargoyles. The external pores in the Mayumbe nest result from incomplete fusion of the *distal end* of the overlapping upper lip with the wall. This results in the external and internal openings in *A. kisantuensis* being *alternate,* while in the Mayumbe nest they are *opposite.*

The nest from Mayumbe is therefore probably related to the nest of *A. gurgulifex,* as shown by the presence of simple conduits and gargoyles in the lower parts of the nest. However, the different method of gallery construction implies a separate origin from a *gurgulifex*-type nest than the other members of the *porifex* group. It would seem more probable that the origin was separate than that the relation between internal and external openings changed secondarily.

It is impossible to say whether the builders of the Mayumbe nest branched off from a *gurgulifex*-like ancestor before or after the divergence of other members of the group. The latter origin may possibly be suggested by the similarity in the distance between external pores of the Mayumbe nest and the *A. gurgulifex* nest (table 1). These nests are also somewhat similar in shape, being truncated at both ends with more or less straight sides.

Emerson (1952a) derives both the Mayumbe nest and the *A. kisantuensis-A. porifex* series from an ancestor with galleries having opposite openings. However, this would necessitate a secondary rearrangement of the openings in *A. kisantuensis,* which seems unlikely. It is, of course, possible that the two types of galleries may have radiated from an *A. desneuxi* type of nest, resulting in parallel rather than convergent evolution.

The Bas Congo Nest

The *"occultus"* and *porifex* groups have been shown by a number of characteristics to be distinct, separate branches of the genus. The members within each group can also be shown to be related by a number of criteria. Up to this point the phylogenetic order in *Apicotermes* is fairly clear. However, the placement of the Bas Congo nest is rather speculative, although the evidence suggests its early divergence from the base of the *porifex* group. Unfortunately, one must proceed without study of the termites themselves, since no inhabitants have as yet been collected with this type of nest.

The Bas Congo nest is oriented in an envelope of sand. The shagreen network is of the type that is very friable and easily scraped from the wall of the nest. Separate internal parietal slits are present. The ramps are direct and scattered. In these characteristics, this nest agrees closely with the *porifex* group.

The shagreen network, although friable, is very heavy and uniformly covers the nest surface. The internal slits are less than half-way from the floor to the ceiling and average over 5 mm. in width, by far the widest of any known nest. This is the only type of nest having internal slits appreciably wider than the distance between slits (table 1, fig. 5). These features differ from the *porifex* group.

The low internal slits suggest a relationship to the *"occultus"* group.

The upper lip of the external opening of the conduit projects downward (figs. 1 and 2). The distal end of the overlapping lip usually fuses with the wall only in the lower stories of the nest. Adjacent hoods often fail to fuse laterally, so that there remains between them a vertical slit ending in a pore-like structure at the upper end that is analogous to the external pores of *A. kisantuensis*. Photographs in the papers by Desneux seem to indicate that these vertical slits are alternate with the internal parietal slits. The space partially or entirely enclosed under the overlapping hoods seems to be structurally similar and probably functionally analogous to the circular galleries of other nests. The presence of different stages in the same nest suggests that the galleries are built in a manner somewhat similar to those of the Mayumbe nest and of *A. kisantuensis* nests (fig. 2). This also implies a relationship to the *porifex* group.

The evidence suggests that the Bas Congo nest is related to the *porifex* group, although a close relationship to any of its known members is unlikely. Because of the very wide internal slits, it is probable that the galleries of the Bas Congo nest originated independently from those of the *porifex* group. This species and the main branch of the *porifex* group may have diverged early, before the origin of galleries—the former retaining a heavy shagreen network, while the extent of this layer decreased in the latter. The low conduits, as in the *"occultus"* group, also suggest an early origin of the Bas Congo nest. Divergence of the Bas Congo line from the *porifex* line *before* the origin of galleries seems to be implied by the improbability of the loss of circular galleries followed by a second origin in the Mayumbe nest and in *A. kisantuensis*.

The differences between the Bas Congo nest and the nests of the *"occultus"* group prevent one from contemplating too close a relationship between these.

Another possible origin of this nest should be considered. The ancestors of the Bas Congo nest might have branched off before the divergence of the *porifex* and *"occultus"* groups. These ancestors would probably have been without circular galleries for the reasons already stated.

In his phylogeny, Emerson (1952a) derives all *Apicotermes* nests from a Bas Congo type of nest. However, this would require regression of the somewhat incomplete Bas Congo galleries and a subsequent secondary origin of galleries in the Mayumbe nest, *A. kisantuensis*, and *A. arquieri*. However, the funnels of *A. lamani* could conceivably have evolved by downward extension of the hoods of a Bas Congo-like nest.

Although unlikely, the possibility should be mentioned that the Bas Congo nest may not belong to *Apicotermes* but rather to a closely related genus. Such a supposition does not seem necessary, however, since the difference between this nest and others known to belong to *Apicotermes* is no greater than the difference between some of these other nests.

A Hypothetical Common Ancestor

Present data do not permit more than a speculative reconstruction of the nest of the immediate common ancestor of known species of *Apicotermes*. However, future collections may someday permit a reasonable approach to an accurate reconstruction. The hypothetical common ancestor shown in figure 2 permits one to relate the different groups with the least difficulty.

Because of the considerable difference between the three groups, it seems preferable to attempt to derive them separately from a very simple nest rather than from any nest resembling those of known species. Due to the improbability of regression of galleries followed by a triple secondary evolution of these structures, this ancestor was probably without galleries. The walls of this nest might be visualized as being perforated by discrete

slits, lower than half-way from floor to ceiling. The external openings of these slits would project little, if any, from the surface of the nest. From this type of structure the nest of *A. gurgulifex* and the nest from Bas Congo may be derived independently with no difficulty. This can be seen in figure 2, which suggests phylogenetic as well as developmental relationships.

The funnels of the nests of *A. lamani* may be imagined as evolving by the extension of the upper lip of the external opening of the conduits. These extensions, rather than fusing with the wall at the distal end, as in *A. kisantuensis,* would fuse to the wall at their sides, thus forming funnels.

The origin of the *A. arquieri* nest is difficult to visualize from any beginning. It is impossible to derive it from any known nest, although a highly speculative derivation may be obtained from the ancestor postulated here. If the *lower lip,* rather than the upper lip as in other species, were to be extended downward and fuse with the wall, the structure of *A. arquieri* nests would result. Lateral connection of adjacent conduits could then have taken place to achieve the continuous conduit characteristic of that nest. The origin of continuous slits may very well have been dependent upon the prior origin of circular galleries. A primary continuity of slits would have provided no wall support, in the absence of an external gallery wall.

Nest Variability and Its Causes

Table 1 shows that the variability between populations of a species varies with the species. Further collections may indicate a greater variability in some of these species. The measurements for two populations of *A. lamani* are seen to be very close. The difference between three measurements of the two Bas Congo populations are not significant. The variability between populations of *A. kisantuensis,* even of the same major type, are seen to be considerable.

The limited amount of material available for this study does not permit a comprehensive view of variability within each species. The differences between species and between the major types of *A. kisantuensis* and *A angustatus* are undoubtedly of genetic origin. However, some of the differences within a species or colony may be the result of other factors. Meteorological conditions, soil composition, nest size, learning(?), population structure, and population size are only a few of the possibilities that come to mind. This question can be settled only by a detailed study of the ecology and behavior of the group.

Schneirla (in Emerson, 1952a) cautions that "similar outcomes may be reached by behavior processes which may have much in common or very little in common." This is also true of morphological characteristics which, although similar, may be either homologous or result from different developmental and physiological processes. However, there is nothing to suggest that a particular type of *Apicotermes* nest is not the work of a single species or that a single species builds more than one type of nest. In no case have different types of nests been found inhabited by the same species of termite. Neither has the same type of nest been found associated with different species. Zoogeographical and ecological data, although not extensive enough to provide much positive evidence, at least are in no way in conflict with the phylogeny presented here. In other words, the ethological data are corroborated by morphological, zoogeographical, and ecological data.

Discussion

There is no evidence to contradict the assumption that nest-building behavior in termites is innate and instinctive. Certainly, colony founding by a single pair of reproductives would eliminate the possibility of workers (which appear only

after these reproductives have left the parent colony) learning these behavior patterns from earlier generations of workers. Innate or instinctive behavior is considered here to be those movements or acts, occurring in response to a specific set of stimuli, for which previous performance as a result of these stimuli is not necessary for the functional completeness of the neural pathways controlling that behavior. The repetition of the behavior pattern, in such instances, is initiated by genetic factors passing from one generation to another through the germ plasm. Lehrman (1953) seems to consider most behavior learned. However, his reasoning is rather difficult to follow and his arguments seem to be largely semantic. Although criticizing the use of "instinct," he offers no adequate substitute.

Teleology and anthropomorphism have no place (when used literally) in the study of innate behavior. An extreme example of such use is seen in a paper by Bugnion (1927). For instance, in discussing the evolution of defense behavior in termite soldiers, he says that "the origin of most of these instincts is a reasoned and conscious action."

Emerson (in Allee *et al.*, 1949) states that "the evolution of behavior results from similar forces and follows patterns similar to those characteristic of morphological evolution, and . . . both depend upon physiological development and genetic interactions." As early as 1898, Whitman (1899) remarked that "instinct and structure are to be studied from the common standpoint of phyletic descent."

To a certain extent behavior is determined and modified by the physiological (e.g., hormonal) processes and the morphological equipment of the organism. Behavioral changes would therefore be expected to parallel evolutionary, genetic changes in morphology and physiology. Evidence also indicates direct genetic changes of the nervous system itself. Further discussion of this subject is beyond the scope of this paper. An excellent general review of ethological evolution is given by Tinbergen (1951, chaps. 7 and 8).

A remarkable difference is seen between the degree of radiation of behavior and structure in the two neuter castes of termites. The morphological features of the workers show minimum radiation. Such conservative characters are of great value in determining the relations between genera and higher categories, but are relatively useless in species identification. On the other hand this caste shows considerable variation of behavior, as illustrated by the many nest types already known for *Apicotermes*. In contrast, the soldiers show considerable morphological adaptation, hence proving the most useful specimens for species determination but often being of less value than the morphologically conservative workers for relating higher categories. The known behavior differences of soldiers within a genus are relatively small.

Nest-building behavior in *Apicotermes* illustrates particularly well several principles analogous to structural evolution. These will be discussed in greater detail.

Adaptation

The nests of termites have obviously evolved toward a high degree of social homeostasis, providing considerable regulation of the environment (e.g., temperature and humidity) and protection from enemies (e.g., predators and fungi).

A high selective advantage of the various systems of wall perforation is indicated by their occurrence in all known nests of *Apicotermes*, with the exception of *A. "occultus."* It is generally assumed that the function of such structures is to permit the exchange of gases between the interior and exterior of the nest (Desneux, 1953; Emerson, 1953). Although there is no supporting experimental evidence, this seems to be a safe assumption, for the carbon dioxide tension in such underground nests must become very high, and the oxygen tension rather low.

However, the assignment of a particular function to a structure without experimental verification sometimes involves a certain degree of hazard. This is suggested here by the fact that although the function of the perforation systems as a whole seems to be for gas exchange, the evidence concerning the specific function of the circular galleries within this system is rather contradictory. The importance of the galleries cannot be denied, for they appear to have originated independently four times.

Certain factors suggest that the function of the circular gallery may be something other than gas exchange *per se*. A preliminary experiment has been made comparing the rate of diffusion across models of the walls of various species of *Apicotermes* nests. The meager data thus far obtained suggests that the galleries may have little or nothing to do with the rate of diffusion, this apparently being determined (as might be expected) by the size of the smallest parietal opening (in most cases the external opening). If this is at all indicative of the actual situation, it is interesting to note the possible significance of the decrease in conduit width in the *A. kisantuensis-A. porifex* series. If diffusion is proportional to the perimeter of the smallest (external) opening of the gallery, the larger size of the internal slit would be of no advantage to the species from the standpoint of gas exchange. Therefore a narrowing of the conduit could take place without adverse effects upon the "ventilating system" but possibly with some advantage such as increased protection from water, predators, or fungi. Such a possibility is also consistent with the presence of wide conduits in *A. gurgulifex* and *A. desneuxi*—both without galleries (and without the small external openings of galleries) and therefore able to take full advantage of the greater rate of diffusion offered by wide slits. In the case of nests with galleries, the lower rate of diffusion would presumably be compensated for by added protection. It cannot be overemphasized, however, that the experiment mentioned here was preliminary and the result can be considered no more than suggestive. Additional work with this method is in progress and it is hoped that it may give some instructive results.

The somewhat similar nests of the South American termite *Procornitermes lespesii* also have circular galleries and are subterranean in hollow cavities (Emerson, 1952b). However, the galleries of these nests have neither internal nor external openings (apparently never had them) and therefore could not function directly for gas exchange (except possibly to produce thinning of the wall). It is, of course, possible that the function of the galleries in *Procornitermes* may be entirely different from that in *Apicotermes*.

The regulation of internal nest temperatures against external fluctuations has been suggested as a possible function of the galleries (Desneux, 1953; Emerson, 1952b). It is questionable, however, whether the relatively slight temperature changes to which these termites are subjected, being subterranean and tropical, would provide the selective pressure for the evolution of such apparently important structures. It is difficult to see how the primitive stages of gallery evolution could provide increased temperature control. Maintenance of high temperatures within the nest could also be a function, although this would meet with some of the same objections just noted concerning possible protection from external temperature changes.

Desneux (1953) suggests that the nests of the *A. kisantuensis-A. porifex* series, once completed, may be enlarged according to the spatial needs of the inhabitants. He shows several photographs suggesting that secondary galleries may be built on the outside of a completed nest and that the inner, original galleries may then be removed. The evidence for this is still not conclusive, however. It has been found that at least some species of *Apicotermes* have colonies composed of a num-

ber of nests of various sizes (Desneux, 1953; Grassé and Noirot, 1948b). Grassé (1952) considers colony enlargement to take place by addition of another nest. Perhaps colony growth takes place by both of these methods.

Thus it appears that the direct participation of circular galleries in the regulation of gas exchange across the nest wall is open to serious question. The most likely function seems to be protection of the conduits from soil water, predators, fungi, parasites, or some other factor. Such a function would not be inconsistent with the apparent method of origin. The overlapping upper lip (possibly lower lip in *A. arquieri*) could quite conceivably provide protection for the conduits even though a function of temperature or diffusion regulation is more difficult to imagine. Protection, especially from water, is also suggested by the downward slanting funnels of *A. lamani*. The conduits of most species also slant downward and outward. An exception to this is the inward slanting continuous conduits of *A. arquieri*. It should be noted, however, that none of the present evidence on the function of the galleries is adequate, and a final answer to this problem must await further data. These structures may even function in several ways or have changed their function during the course of their evolution.

The partial closure of internal parietal slits by sand and mortar has already been noted as interfering with slit measurement. Because of the variation in the degree of closure within a nest and between nests from different localities, Desneux (1953) has suggested that the degree of closure may be determined by local gas exchange needs. If such a regulation exists, it would be impossible at present to know whether the degree of slit closure is irreversibly determined by the conditions present when the slits were originally built, or whether they may be later modified as environmental conditions change.

As the field of ethology advances, it might be expected that behavioral homeostatic mechanisms will be found to be more common. A few such mechanisms known for other groups of animals will be mentioned here. Richter (1942–1943) has shown that certain surgically produced hormone deficiencies in rats would modify the animal's dietary preferences in such a way as to largely compensate for the physiological disturbances caused by the operation. For instance, if a parathyroidectomized rat was provided with both ordinary water and water with calcium added, it would drink sufficient amounts of the calcium water to prevent excessive symptoms due to the removal of the parathyroid. He also found that hypophysectomized rats, now incapable of adequate heat production, built much larger nests than normal animals.

Some of the well known homeostatic mechanisms of bees have been reviewed by Chauvin (1954). For instance, periods of increased activity during the winter prevent the temperature of the cluster from dropping to a fatal low, and by fanning, bees are able to increase air circulation within the hive.

Convergence

If the phylogeny presented here is approximately correct, the circular galleries probably have evolved independently four times. The two main branches, the *"occultus"* and the *porifex* groups, are quite different and the lowest member of each branch is without these structures. The galleries of the Mayumbe nest have been shown to be formed in a manner peculiar to that nest and therefore have probably evolved independently. The Bas Congo nest, although uncertain as to position, seems to have arisen from stock without galleries and is not very closely related to other groups with galleries.

Although examples of convergent evolution are numerous, few show such repeated convergence within a single genus. For instance, the presence of striking display behavior by the males of certain

species of crabs, squid, fish, lizards, and birds is noted by Tinbergen (1953). Social parasitism is found among the cowbirds, cuckoos, weavers, honey-guides, and ducks (Friedmann, 1929). Mimetic resemblances are also known (Cott, 1940). Mosauer (1930, 1935) has discussed the similarity in locomotion on loose sand of the sidewinder of the Southwest United States and the African sand viper of the Sahara Desert. Friedman (1946) notes that the African pipit (*Macronyx*) and the American meadow-lark (*Sturnella*) show a number of ethological (e.g., song, nests, turning away from an approaching observer) as well as morphological similarities. Rain-shedding structures have evolved independently in nests of the Amitermitinae, Termitinae, and Nasutitermitinae (Emerson, 1938). The similarity of the nests of *Procornitermes* and *Apicotermes* has already been noted (Desneux, 1953; Emerson, 1952b). Cases of convergence within a single genus are more easily found for morphological than for ethological characteristics; for instance, the independent origin of terminal tail rackets in two birds, *Dicrurus remifer* and *D. paradiseus* (Mayr and Vaurie, 1948).

Regression

The modern theory of regressive evolution is based largely on the following factors (Emerson, in Allee *et al.*, 1949):

1. Most genes (pleiotropic) affect more than one character.
2. Most characters (polygenic) are affected by more than one gene.
3. Each gene mutates at a specific statistical rate.
4. Most mutations are deleterious.
5. Entire organisms or populations are selected, as well as the parts of each.

A structure, physiological process, or innate behavior pattern would be expected to remain functional as long as it is maintained by a positive selection pressure. Loss or reduction of this positive pressure may lead to regression. Such loss or reduction might result from an environmental change, bringing about conditions to which the character is not as well adapted, or under which it is detrimental. In the latter case there would be a negative selection pressure against the character. However, regression may also occur in the absence of negative pressure (Wright, 1929). Wright (in Emerson, 1938) states that "the type allele in each series is that which has the most favorable net effect on all characters. If one character loses in importance relative to others, there will be a shift in the alleles in many series with degeneration of the character losing importance as a consequence of the increased development of the others." Therefore a neutral character will eventually regress because of the lack of positive selection pressure maintaining it and because of the shift of alleles in favor of other characters. Regressive evolution is thus seen to bring about increased total adaptation rather than decreased adaptation as the term "degeneration" so often seems to imply. This theory explains not only the loss of characters, but also the temporary retention of neutral or slightly detrimental characters. Because of the large number of genes involved in any one character, the generally slow rate of mutation, and the fact that most mutations are deleterious, the regression of a character (through the shift of alleles mentioned above) would be expected to take considerable time.

The isolation of galleries in the nests of *A. "occultus"* seems to have resulted from the regression of wall perforations (Desneux, 1953; Emerson, 1953). Neither internal nor external gallery openings are present. The galleries themselves also seem to be on the way out, since they frequently end blindly rather than continue around the entire circumference of the nest. The closest known relative, *A. arquieri*, has complete galleries with somewhat regressed internal and external openings, and it seems more likely that the galleries of this species

have evolved in the manner already suggested than that they evolved from the isolated galleries of *A. "occultus."*

It seems likely that the wall perforations of *A. arquieri* may also be in the process of regression. Only a few of the external pores are entirely open—the rest being absent or appearing only as slight depressions. The height of the continuous conduit is less than the discrete conduit height of most of the other nests. The walls of the conduit are rough and granular. The granularity of the upper and lower surface may come into contact, although small spaces remain between the surface projections. The internal slit appears to be basically continuous. However, closer observation shows it to be closed at irregular intervals by bits of mortar, so that actually it is open for only about one-half of its total length.

Little can be said at present concerning the cause of this regression. Both species inhabit savanna. The drier soil of the savanna would probably permit greater gas exchange than the soil of the rain-forest, so that wall perforations might be of less value (Emerson, 1952a). Perhaps in the savanna, conservation of moisture within the nest may become of greater importance than gas exchange. Emerson (1953) postulates that the genus originated in the rain-forest, since this is where most of the species of *Apicotermes* and most of the closely related genera are found. It is also possible that these species may have acquired increased tolerance to high carbon dioxide and low oxygen tensions, thereby reducing the adaptive value of wall perforations. A change in porosity of the wall or its orientation in a space rather than in an envelope of sand may also be involved.

Even if the apparent reduction of wall perforations in *A. arquieri* should be found not to be due entirely to regression, the vestigial galleries of *A. "occultus"* will still provide an excellent example of regressive behavior.

The fungus gardens of *Sphaerotermes sphaerothorax* may also be an example of regressed behavior. All other members of the Macrotermitinae that have been studied grow fungi. *S. sphaerothorax* is the only known species of this subfamily that does not raise fungi, although fungus gardens (without fungi) are still built (Grassé and Noirot, 1948a).

Ontogeny

The fact that what appears to be several stages of gallery formation are often found in a single nest and the gradual evolution of galleries as seen in the *A. gurgulifex-A. kisantuensis* series permits a hypothetical reconstruction of gallery ontogeny, although this process has never actually been observed.

It seems quite likely that the construction of the galleries in the Bas Congo and *porifex* groups shows a recapitulation of the evolutionary stages of these structures. Such a recapitulation is not too surprising. In fact, it is difficult to imagine a method of gallery formation more logical or simpler than that illustrated in figure 2. The hypothetical development as well as the evolution of galleries seems to consist basically of the overlapping of the upper lips of the external conduit openings. No stage of this continuous extension could be omitted without disrupting the continuity of the gallery. Therefore, recapitulation, in this particular instance, would seem almost unavoidable. Of course, it is recognized that the phenomenon mentioned here is considerably different than recapitulation in the sense of the appearance of certain ancestral characteristics during the ontogeny of an organism. Here the ancestral stages are repeated in an extraorganismic structure rather than in the organism itself; the repetition is not associated with the development of an organism but with a "full-grown" organism (the worker termite); and the nest is produced not by an individual organism but by a colony (supraorganism). Perhaps the term "recapitulation" is not even justified here, although its use is conveniently descrip-

tive. It is not meant to imply that recapitulation is necessarily a general phenomenon of ethological development. The recapitulation discussed here extends back only to the *A. gurgulifex* stage. Neither does this recapitulation necessarily imply a similar process in the development of the behavioral equipment of the worker termite.

The nests of *Apicotermes* show radial symmetry. There is radial (e.g., conduits and external pores) and vertical (e.g., galleries, lamellae, and ramps) replication of structure. Emerson (1947) analogizes this replication to the pores in the walls of a sponge of the ascon or sycon type.

Nest regeneration is known among other termites, but has not yet been observed in *Apicotermes*. Emerson (1951) has observed reconstruction in a *Cubitermes intercalatus* nest in the Belgian Congo. Hingston (1932) has made experimental observations on behavioral regeneration of rain-shedding ridges of a *Constrictotermes cavifrons* nest. Grassé (1937) has observed workers of *Macrotermes* (= *Bellicositermes*) repairing holes that he had broken in the nest. Certain cocoon-building insects are also capable of repairing these structures to some extent. Van der Kloot (1953) has shown that the Cecropia silkworm is able to rebuild destroyed parts of the outer layer of the cocoon, if it has not yet begun work on the inner layer.

Grassé (1937) notes that nest enlargement (analogous to the growth of an organism) takes place in some termites. In *Macrotermes* (= *Bellicositermes*), the application of new mortar to a part being enlarged seems to be preceded by a destruction of the wall in that area. The presence of a royal cell relatively high above the ground also indicates that this part of the nest must have been moved during the growth of the nest. This might involve some reorganization of the nest interior as well as enlargement. Emerson (1938) illustrates the enlargement of a nest of *Nasutitermes quayanae* by additions of cells on the outside.

The Supraorganism

Emerson (1952a, in Allee *et al.*, 1949) has used *Apicotermes* to illustrate the principle of the supraorganism. Schneirla (1946) objects to the use of analogies between different levels of organization. He says:

> "It is questionable whether the deductive leaps of the analogy method provide a legitimate means of studying the past history of animal societies or the nature of their present integrations. . . . Analogical procedures such as those involved in using the 'superorganism' concept are not adequate for studying social levels comparatively."

However, Emerson has defended both the supraorganism concept (1952a) and the use of analogy (1952a, 1954). He (in Allee *et al.*, 1949) makes the following comment concerning analogy:

> "It is true that in comparing distinct integrative levels, homologies (resemblances with a common genetic basis) cannot be assumed, although we have seen . . . that the identical mechanisms of one level may sometimes integrate a higher level. Similarities may, however, be convergent and therefore analogous, and a comparison of similar pressures guiding unlike organisms toward analogous functions is significant."

Boyden (1947) objects to the application of the term homology to ethological similarities because of the frequent difficulty in demonstrating a common ancestor and because of its original restriction by Owen to morphological similarities. However, such a view would seem to overlook the value of the term in indicating common origins and genetic similarities.

The evolution and radiation of the complex nests of *Apicotermes*, built by sterile workers, can be explained only by the selection of the entire colony as a unit. Such group selection is also seen in the evolution of the worker and soldier castes of termites. Worker sterility also eliminates the possibility of Lamarkian influences on the evolution of such charac-

ters as nest-building behavior. Darwin (1877, pp. 230–233) and Weismann (1893) were among the first to recognize the evolutionary significance of "neuter" castes.

The Use of Behavior in Building Phylogenies

In any study of phylogeny it is of the utmost importance to use and correlate all available data from all available sources. A failure in this respect is seen in Kemner's (1927) classification of Javanese termite nests and the classification of caddis flies (based upon feeding behavior and case) by Milne and Milne (1939). Although these workers present valuable information concerning the constructions of these insects, Emerson (1938 and personal communication) notes that their phylogenies based upon behavior are not verified by the morphological data. Since both behavior and structure have evolved by similar methods, one is not *a priori* more important than another in determining phylogenetic relationships. A truly accurate phylogeny must be able to accommodate data on all organismic characteristics. Obviously the structural properties of an organism have not evolved completely apart from its behavior. Selection, of course, is applied to each whole integrated organism or organismic unit such as the supraorganism.

The importance of behavior as an indicator of phylogenetic relationships is finally being recognized. The use of behavior in this manner emphasizes the similarities between the evolution of ethological and morphological characters. So far, relatively few studies of comparative behavior relate more than a small number of species. More investigations comparing large numbers of closely related species are to be desired. A few interesting studies will be briefly noted here.

Emerson (1938) has made a comparative study of termite nests largely at the family and generic level. He also deals with the nest-building behavior of the termites themselves and discusses the evolutionary implications of termite nests. Many of the papers of Grassé and of Grassé and Noirot deal with termite nests and nest-building behavior [e.g., the construction of the royal cell in *Cephalotermes rectangularis* (Grassé, 1939)]. Grassé's 1944 paper on the nests of the Macrotermitinae shows that behavior may also characterize higher taxonomic categories.

An outstanding study of the evolution of behavior is the work of Lorenz (1941) on the calls and mating behavior of some of the Anatinae. His diagram of the phylogenetic relationships between the species studied correlates a number of morphological as well as behavioral characteristics. In some cases he has been able to arrange series, showing the evolution of a highly modified behavior pattern from a more primitive pattern. Delacour and Mayr (1945) state that such ethological characters as pair formation, displays, nesting and feeding habits, are of more value than certain previously emphasized morphological characters. For instance, bill shape is so adaptive that it can be used for little more than species identification.

Petrunkevitch (1926) notes the value of such characteristics as type of web and manner of caring for the egg cocoon for spider classification. Early workers in the field were often over-enthusiastic in their use of behavior, occasionally making errors resulting from the confusion of analogous with homologous behavior. This again emphasizes the importance of using all available evidence in building a phylogeny.

Friedmann (1929) finds that the phylogenic series, *Agelaioides badius—Molothrus rufo-axillaris—M. bonariensis—M. aster,* is indicated by nesting behavior and song as well as by zoogeography and structure. The first bird in this series has no courtship display, incubates its own eggs which are laid in the nests of other birds, and has a "primitive, formless type of song." The next two species show a simple courtship display, are parasitic,

and have a more or less typical cowbird song. The last in the series has a more elaborate display, is parasitic, and has a clearer song. The behavior of two captive young males of *M. aster* is of interest. The development of mating behavior during their first spring showed a recapitulation of the behavior of their more primitive relatives until the adult behavior typical of the species was finally exhibited. These birds had been raised in the absence of others of this species. Friedmann (1948) makes a similar report on the parasitic breeding habits of African cuckoos. However, the data are not as complete as in the case of cowbirds.

Davis (1940, 1942) has studied the communal nesting behavior of the Crotophaginae (the Anis), a South American subfamily of the cuckoos. He arranges the four species in the order: *Guira guira —Crotophaga major—C. ani* and *C. sulcirostrus*. The community in the first species consists of a number of separate pairs of birds which may sometimes nest separately and defend a small territory within the territory of the flock. In the second species, the pairs unite to defend the flock territory and the group builds a single nest. In *C. ani,* polygamy and promiscuity prevail and the pair defense is replaced by colonial defense of territory. Communal nesting seems to be related to parasitism, so common in other branches of the cuckoos. This is suggested by the fact that *Guira* has been reported to lay eggs occasionally in the nests of other birds.

The phylogeny of *Drosophila* has probably been studied by more methods than has that of any other group. To these methods may be added the studies of Spieth (1952) on the mating behavior of this group. He found that the ethological data for the species of *Drosophila* that he studied closely paralleled the data from other methods. He also has suggested a hypothetical ancestral mating pattern.

The identification of caddis fly larvae is greatly facilitated by the cases built by so many of them. Identification is often made on the basis of case alone, little attention being paid to its inhabitant. For instance, Needham and Needham (1941) give a key to Trichoptera larvae, based mostly on case characteristics.

Crane (1941) has made extensive studies of the crab *Uca*. She makes the following statement concerning their courtship display:

> "Each species proved to have a definite, individual display, differing so markedly from that of every other species observed, that closely related species could be recognized at a distance merely by the form of the display. Furthermore, related species had fundamental similarities of display in common, and series of species, showing progressive specialization of structure, in general showed similar progression in display."

Chapin (1917) found that the generally accepted classification of the Ploceidae, based mostly on the length of the tenth primary, was largely artificial. In both subfamilies (as regrouped by Chapin) there appeared to be a convergent shortening of this feather. In regrouping the members of this family, Chapin made considerable use of nesting behavior. In one of his subfamilies pensile, intricately woven nests are found, while in the other subfamily nests are neither pensile nor woven.

Summary

Termite nests are species-specific products of the nest-building behavior of the colony. The subterranean nests of *Apicotermes* provide unique material for the study of the evolution of behavior. Each species builds a very specific type of nest which shows distinct similarities to and differences from nests of other species of the genus. Nest characters show phylogenetic relationships more clearly than do the morphological characteristics of the termites. Nest-building behavior in termites is probably entirely innate or instinctive, at least according to the definition of "instinct" given here. Ethological evolution seems to be directed by the same forces as is morphological evolution. The nests of *Apicotermes* show particu-

larly well several phenomena found also in the evolution of structural characteristics. Termite nests have evolved toward a high degree of social homeostasis, providing considerable regulation of the environment and protection from enemies. Wall perforations, apparently functioning to permit gas exchange between the interior and exterior of the nest, must be of considerable adaptive advantage, since they occur in the nests of all but one species of *Apicotermes*. Circular galleries possibly function by protecting these perforations from ground water and enemies that might otherwise enter the nest. Galleries may have evolved convergently as many as four times within the genus. Vestigial, partially regressed galleries are seen in one nest that has completely lost the openings of the galleries. Another nest seems to be in an earlier stage of this regression. The apparent method of gallery construction within a single nest seems to recapitulate stages in the evolution of these structures. These nests show radial symmetry and replication of structures. *Apicotermes* provides an excellent illustration of the supraorganism concept.

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A PRELIMINARY REPORT ON THE GENETICS OF THE MACHAON GROUP OF SWALLOWTAIL BUTTERFLIES

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INTRODUCTION

Evolution has been studied in considerable detail from the theoretical point of view. However, little attention has been paid to the actual genetic differences which have arisen between species and subspecies of animals in the course of their evolutionary history, although some work has been done along these lines (e.g., Ford, 1953; Spurway, 1953). Such an approach is valuable because it allows predictions based on mathematical theory to be checked; an important precaution, as many of the mathematical models are necessarily simplified. Moreover, a knowledge of the genetic differences between species or subspecies can be used to give a measure of the rate at which their evolution has proceeded, if the time of isolation of the two or more diverging forms can be determined from other data.

The present investigation is concerned with the genetic differences which have arisen during the evolution of the swallowtail butterflies (S. F. Papilioninae) closely related to *Papilio machaon* L., particularly those inhabiting the North American continent.

Nomenclature

The genetic relationships between four forms of swallowtails have been investigated. These are *Papilio machaon* L. from Europe, *Papilio brevicauda* Sanders from the area of the mouth of the St. Lawrence in North America, *Papilio polyxenes asterius* Cram. from the Eastern United States and Canada, and *Papilio zelicaon* Lucas from the United States and Canada west of the Rocky Mountains. In the British Museum collections these three American forms together with some others are treated as subspecies of *P. machaon*. Rothschild and Jordan (1906) however, describe *P. zelicaon* as a species separate from *P. machaon*, and include *brevicauda* and *asterius*, together with the forms *americus* Kollar and *polyxenes* Fabr. as subspecies of one species *P. polyxenes*. In a previous paper (Clarke and Sheppard, 1953), we gave specific rank to *brevicauda*, because, judged by the degree of sterility of the hybrids, it is as distinct from *P. p. asterius* as is *P. machaon*. Unfortunately, we have not been able to investigate the differences between *P. p. asterius* and *P. p. americus;* but in view of the fact that they are morphologically quite as distinct as are *P. p. asterius* and *P. brevicauda*, it seems desirable to call them *P. p. asterius* and *P. americus*, so that there will then be no suggestion in the absence of genetic data that *P. americus* is closer to *P. p. asterius* than is *P. brevicauda*.

METHODS

Mating

All the pairings between the swallowtail butterflies have been obtained by hand-mating the individuals. The technique has been described in detail by Clarke (1952). It consists of holding the male and female butterflies together so that their genitalia interlock and copulation takes place.

Measurements

The eye-spot. Two characters of the eye-spot in the anal angle of the hind-wing were measured. These were: (1) the length and depth of the black area of scales which forms the pupil of the eye-spot in the American species and the

black posterior border of the red area in *P. machaon*. (2) The depth of the area of black scales forming an anterior border to the eye-spot and also the depth of the red area. The measurements were taken from the underside of the left wing. Only if this was damaged was the right wing used.

The depth of the black area (often with blue scales on it) at the anterior border of the eye-spot was measured from a point at its anterior border (fig. 1B, *b*). This was found by constructing a line from *a* to the inner margin of the wing at right angles to "vein" 2. From the mid-point of this a second line *bcd* (fig. 1B) was made parallel to the "vein." The measurement was taken from *b* in a posterior direction to a position where red scales replaced the black (fig. 1B, *c*). The depth of the red area was measured from this point to the border of the red area at the posterior end of the eye-spot or to the posterior border of the black pupil if this obscured the border of the red area (fig. 1B, *d*). When the point of junction between the red and black areas at *c* is obscured by blue scales, the position can be accurately found from the change in colour of these scales, from dark blue (over black) to light blue (over red).

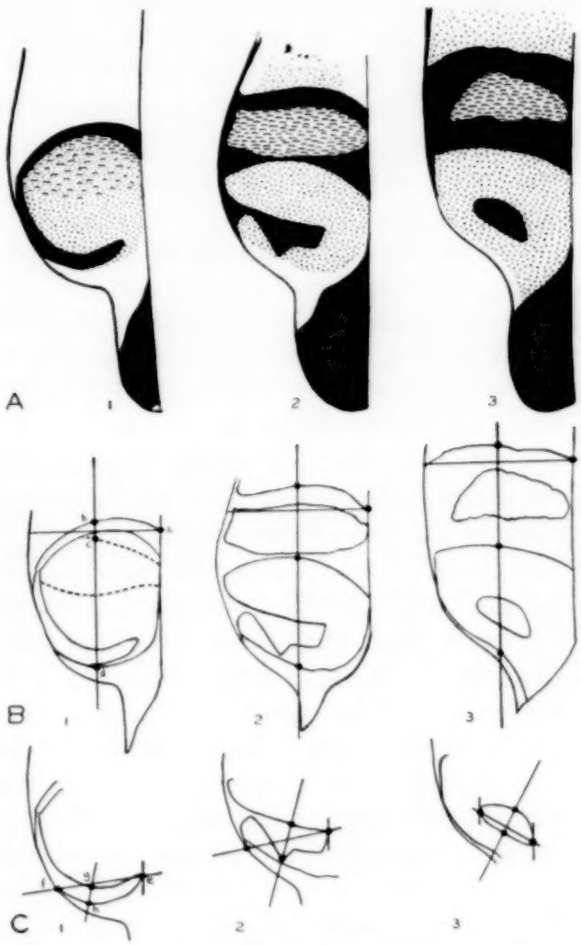

FIG. 1. A (1) shows the eye-spot of *P. machaon*, (3) the eye-spot of *P. p. asterius* and (2) an F.1 hybrid, chosen because the pupil in this specimen is particularly difficult to measure. Black indicates an area of black, white of yellow, dots of red, lines of blue and black mixed, and dots and lines of red and blue mixed. B gives the points between which the depths of the black area, *bc*, and red area, *cd*, are measured. C gives the points between which the depth of the pupil, *gh*, and its length, *ef*, are measured. The method of constructing these lines is given in the text (pages 183 and 184).

The depth of the black pupil (or posterior black border) was measured at its widest point along a line cutting its anterior and posterior borders at right angles (fig. 1C, *g–h*). The other measurement of the pupil was taken from the point (fig. 1C, *e*) nearest to "vein" 2 (CuIb of Tillyard (1919)), towards the inner margin of the wing. When the black area formed a border to the eye-spot (fig. 1C, 1) the measurement was made to that place where it met the inner margin of the wing posteriorly (fig. 1C, *f*). When the black line was interrupted by red scales before this point was reached, the measurement was taken up to the interruption (fig. 1C, 3).

Colour of the larval spots: The colour of the larval spots was scored at two different periods, (1) just after moulting to the last larval instar and (2) when the larva was fully grown just before pupation. At the first period the spots were scored as either yellow or some shade of orange or red. At the second, they were divided up into three groups, red (or dark orange), pale orange and yellow. The last two categories were always found to come from individuals that were scored as yellow at the earlier period, and

the reds from those that had previously been scored as orange or red. In the later experiments the larvae, when fully grown, were matched against the colour atlas of Villalobos and Villalobos (1947). This had the advantage of allowing the colour to be recorded by three sets of figures (for hue, value and degree) so that larvae scored in different months or years could still be accurately compared one with another.

Results

Up to the present time (December 1953) the following hybrids have been obtained between the forms investigated: *asterius* ♀ × *machaon* ♂, *machaon* ♀ × *asterius* ♂, *brevicauda* ♀ × *machaon* ♂, *brevicauda* ♀ × *asterius* ♂, *asterius* ♀ × *brevicauda* ♂, *zelicaon* ♀ × *machaon* ♂, *machaon* ♀ × *zelicaon* ♂, *asterius* ♀ × *zelicaon* ♂, *zelicaon* ♀ × *asterius* ♂, and *brevicauda* ♀ × *zelicaon* ♂.

All these hybrids except those between *zelicaon* ♀ × *asterius* ♂ and *brevicauda* ♀ × *zelicaon* ♂ have been described by Clarke and Sheppard (1953). That between *brevicauda* ♀ × *zelicaon* ♂ is still in the pupal stage; the other undescribed hybrid is found to be indistinguishable from the *asterius* ♀ × *zelicaon* ♂ hybrid. In fact no difference depending on the species of the female has been found between any of the hybrids. All have the same appearance as the off-spring of a reciprocal cross.

In the present investigations, only some of the differences between species have been studied genetically and these are listed below.

1. The ground-colour of the wings is either yellow or black. If it is yellow, the body of the butterfly is also yellow with longitudinal black bands on it. If it is black, the body is also black with a number of rows of yellow dots on it.

2. If the ground-colour of the wings is yellow, then the pattern of marks on the wings is very similar in the two sexes. If the ground-colour is black there is usually sexual dimorphism with regard to the distribution of black and yellow on the wings, the females being much blacker than the males, due to a reduction in the width or an absence of the proximal band of yellow spots, as in *P. p. asterius*. However, in some species there is no marked sexual dimorphism, as, for example, in *P. brevicauda* in which both sexes much resemble the males of *P. p. asterius* with respect to this character.

3. Under the forewing, particularly at the apex, there is a large number of yellow scales forming a yellow smudge in *P. machaon* and to a lesser extent in *P. zelicaon*. These scales are not present in *P. p. asterius* and *P. brevicauda* (in some individuals a few yellow scales are present).

4. The legs of the various forms are either black or have yellow as well as black on them. To understand the genetics of this situation, it is necessary to consider the colour of the femur separately from that of the tibia.

5. Most of the "cell" of the forewing on the underside is yellow in *P. machaon* but black in the other three species.

6. In all four species, the eye-spot on the anal angle of the hindwing has either a central pupil (the three American species) or a black posterior border (*P. machaon*). The shape and area of the eye-spots also vary. In *P. machaon* the area of red tends to be larger than in the other three species and extends slightly further anteriorly. Moreover, the black area of scales at the anterior border of the red is reduced in width and some of the blue scales come to lie within the red area.

7. The four sub-marginal lunules on the underside of the hind-wings above the tail are either yellow or orange.

8. The full-grown larva, which is green with black transverse bands, has either yellow or red (sometimes orange) spots on these bands.

In table 1 the differences between the species are set out for comparison.

TABLE 1

	1 ground-colour	2 sexual dimorphism	3 yellow apical spot	4 legs	5 "cell"	6 eye spot		7 lunules	8 larval spots
						pupil	anterior border		
P. machaon	yellow	absent	marked	partly yellow	yellow	absent	narrow	yellow	red
P. zelicaon	yellow	absent	reduced	black or nearly black	black	present	broad	yellow	red, pale orange or yellow
P. p. asterius	black	present	absent	black	black	present	broad	orange	yellow
P. brevicauda	black	absent	absent	black	black	present	broad	orange	yellow

The hybrids between the various species have been described with regard to these characters by Clarke and Sheppard (1953). Until the present time all sib matings of the F.1 hybrids have proved entirely infertile. Only after at least one backcross have fertile sib matings ever been obtainable. It has been difficult to get the most useful crosses, not only on account of infertility, but also because of a scarcity of suitable living material. As a result of this, the pedigrees of various insects

TABLE 2

mating	parents female		parents male	genotypes	Black males	Black females like males	Black females unlike males	pupae remaining
1	a	×	m	BB×bb	40	0	24	
2	a	×	m	BB×bb	11	0	9	
3	a	×	m	BB×bb	7	0	6	
4	a	×	m	BB×bb	1	0	2*	
5	a	×	m	BB×bb	2	0	1	
6	m	×	a	bb×BB	2	0	5	
7	m	×	a	bb×BB	2	0	2	
8	m	×	a	bb×BB	7	0	6	
9	m	×	a	bb×BB	12	0	14	
21	b	×	m	BB×bb	1	0	0	
22	b	×	m	BB×bb	0	2	0	
25	a	×	z	BB×bb	2	0	0	
26	z	×	a	bb×BB	2	0	1	
27	b	×	a	BB×BB	7	8**	0	
31	a	×	b	BB×BB	4	0	0	
43	b	×	z	BB×bb	0	0	0	1
28	a	×	27	BB×BB	3	0	2	1
29	28	×	28	BB×BB	5	0	4	1
30	b	×	27	BB×BB	2	1	0	
42	29	×	29	BB×BB	1	0	0	1
11	6	×	a	Bb×BB	0	0	4	
35	16	×	a	Bb×BB	10	0	6	
12	11	×	m	BB×bb	4	0	9	

* In this brood two gynandromorphs appeared together with the insects listed.

** These 8 black females were not identical in appearance with the males but did not show the extreme sexual dimorphism of *P. p. asterius* females.

have become very complicated in some instances and to simplify the tables, all matings are given a number. When one of the original four forms is a parent, its species is indicated by a small letter (m = *P. machaon*, z = *P. zelicaon*, a = *P. p. asterius*, b = *P. brevicauda*). If, however, a parent is derived as a result of hybridization, the number of the mating, of which it is an offspring, is given so that from the table the pedigree of every individual can be traced.

The Genetics of Black Ground-Colour

All F.1 hybrids are black if one of the parent species has wings with a black ground-colour. When the other parent is yellow and the hybrids are backcrossed to a yellow individual there is a 1 : 1 segregation in the next generation (tables 2, 3 and 4). This suggests very strongly that a single pair of genes is involved. Moreover, a sib mating between two black individuals (after one or more backcrosses to yellows) irrespective of the species used gives a ratio of black to yellow not significantly different from 3 : 1. It will be seen from tables 2, 3 and 4 that the assumption that the black ground-colour is controlled by a single dominant gene is in accordance with all the facts, and there is no evidence of any disturbance in the expected ratios as the result of hybridization. Consequently, it has

TABLE 3

mating	parents female		male	genotypes	Yellow males	Yellow females like males	pupae remaining
32	z	×	m	bb×bb	6	3	
33	m	×	z	bb×bb	3	0	4
14	13	×	m	bb×bb	0	1	
15	14	×	m	bb×bb	0	1	
20	16	×	16	bb×bb	4	4	
34	33	×	m	bb×bb	0	1	
41	39	×	38	bb×bb	15	11	

TABLE 4

mating	parents female		male	genotypes	Yellow males	Yellow females like males	Yellow females unlike males	Black males	Black females like males	Black females unlike males	pupae remaining
10	m	×	5	bb×Bb	3	1	0	3	0	1	
23	m	×	21	bb×Bb	4	2	0	2	0	0	8
24	m	×	23	bb×Bb	1	2	0	0	0	1	
13	6	×	m	Bb×bb	0	1	0	0	0	0	
16	9	×	m	Bb×bb	12	14	0	18	0	10	
17	9	×	m	Bb×bb	2	2	0	3	0	6	
18	9	×	m	Bb×bb	6	4	0	7	0	3	
37	24	×	m	Bb×bb	1	1	0	0	0	4	
38	37	×	m	Bb×bb	3	5	0	5	0	3	
39	37	×	m	Bb×bb	3	3	0	0	0	1	
40	38	×	m	Bb×bb	3	3	0	8	0	3	
44	17	×	m	Bb×bb	2	5	0	0	0	0	
45	17	×	m	Bb×bb	1	0	0	0	0	2	
19	16	×	16	Bb×Bb	1	4	0	7	0	11	
36	19	×	19	Bb×Bb	0	1	0	2	0	1	
48	19	×	19	Bb×Bb	9	3	0	10	0	9	

been possible to insert in the tables the genotype with respect to ground-colour of all the parents of the broods.

The proximal band of yellow spots on the wings of both *P. brevicauda* and *P. p. asterius* is distinct, each spot having a relatively well defined outline. However, the spots in the F.1 hybrids between *P. p. asterius* or *P. brevicauda* and *P. machaon* or *P. zelicaon* have a less clear-cut outline on their inner border. A hybrid with *P. machaon* after one or more backcrosses, has reduced spots as a result of the extension of the black, and the border of the yellow badly defined because of a scattering of black scales among the yellow ones. It appears that both *P. machaon* and *P. zelicaon* carry modifiers which tend to increase the area of black in the presence of the gene *B* and destroy the clear outline of the yellow spots. This suggests that, in *P. p. asterius* and *P. brevicauda,* the pattern of yellow as such may be important and that a gene-complex has been selected which gives the yellow area a distinct outline.

Sexual Dimorphism

P. p. asterius is sexually dimorphic for wing pattern, the inner band of yellow spots being much reduced or absent as a result of the extension of the black ground-colour in the female. *P. machaon* does not show this dimorphism, which could not in fact appear, as the black ground-colour is not present and therefore could not obliterate the yellow. Consequently the yellow individuals produced by backcrossing black heterozygotes to yellow homozygotes do not show this sexual dimorphism (table 4), whereas it is present among the black individuals. *P. brevicauda,* unlike *P. p. asterius,* does not show the dimorphism, the females being like the males in pattern. Moreover, the hybrid between *P. brevicauda* and *P. machaon* also does not show sexual dimorphism. The backcross of this hybrid to *P. machaon* has not yet produced any black females, although it may do so as eight pupae from the mating concerned still remain to emerge (table 4, mating 23). However, a black male from this brood when backcrossed to *P. machaon* (table 4, mating 24) produced a black female whose wing pattern was similar to that of a female *P. p. asterius* on the upper surface. No black males were produced, but further backcrosses to *P. machaon* using this black female and its offspring show that the dimorphism has appeared (table 4, matings 37, 38, 40).

This result shows that the presence of the dimorphism in *P. p. asterius* but not in *P. brevicauda* is not due to the presence of different genes controlling the black ground-colour, but is a reflection of the differences in the residual gene-complex of the two species. It is not yet clear from these matings whether the presence or absence of the dimorphism is under the control of one or more than one gene, as no black females have yet emerged from the critical brood. However, it can be said that *P. machaon,* although itself not sexually dimorphic for this character, has a gene-complex producing the sexual dimorphism in the presence of the dominant gene determining the black ground-colour.

In the hybrids between *P. brevicauda* and *P. p. asterius* there is some sexual dimorphism although it is not as great as in *P. p. asterius* itself. This shows that *P. p. asterius* and *P. machaon* differ with respect to the genes controlling the expression of the dimorphism in the presence of the dominant gene *B*, but still does not show if many genes or one major gene with modifiers, is involved.

The only female obtained from a mating between *P. zelicaon* and *P. p. asterius* shows the full expression of the dimorphism, so that it is probable that *P. zelicaon,* which has a yellow ground-colour, has a gene-complex giving sexual dimorphism when the gene *B* is introduced into it, as has *P. machaon.*

TABLE 5. *Larval spots*

mating	parents female		parents male	parental phenotype of larva	Red (R)	Pale Orange (P.O.)	Yellow (Y)
Z1	z	×	z	?	0	10	2
Z2	z	×	z	?	7	5	1
11	6	×	a	R×Y	2	0	2
19	16	×	16	R×R	21	11	0
20	16	×	16	R×R	8	4	0
a	16	×	16	R×R	5	1	0
b	16	×	16	R×R	1	0	0
c	16	×	16	R×R	1	0	0
35	16	×	a	R×Y	11	11	0
47	19	×	19	?	13	5	0
36	19	×	19	PO×PO	0	33	14

The Control of Larval Spot Colour

The full-grown larva of *P. machaon* from Europe has red (or orange) spots as has the Japanese subspecies *P. m. hippocrates*. The spots on the larvae of *P. p. asterius* bred by us have always been yellow and they have been described as yellow in *P. p. asterius, P. brevicauda* and *P. zelicaon* from California, by Edwards (1874, 1884). However, they are probably orange in some populations (McDunnough, 1939).

The hybrids between *P. p. asterius* and *P. brevicauda* as well as these backcrossed to either parent species, have always had larvae with yellow spots in the last larval instar. However, any individual, whether a hybrid or one of the other three species, when mated to *P. machaon*, has always produced larvae with red, orange, or pale orange spots, with the exception of two larvae in twenty-nine of Mating 18 which had almost yellow spots. There has been apparent segregation for spot colour in some broods (table 5). The hybrid between *P. p. asterius* and *P. machaon* backcrossed to *P. p. asterius* (Mating 11) produced four larvae, two larvae having red (or orange) spots and two yellow spots. Two broods of *P. zelicaon* have shown segregation, but in one (Z2), five of the individuals were a very pale orange in colour and were different from the true red or yellow individuals. In the other brood (Z1) red was not distinguished from pale orange.

Unfortunately, owing to lack of material, it has been impossible to repeat matings similar to Mating 11 (except for one recent mating p. 190), as *P. p. asterius* has not been available for mating to the hybrids when these were emerging. However, it has been possible to backcross hybrids between *P. machaon* and *P. p. asterius* to *P. machaon* and then obtain sib matings. This has been done with the offspring of Mating 16. Thirteen matings were made (table 10), but only five produced any eggs that hatched; and in only two of the broods (Matings 19 and 20) were any butterflies produced. It will be seen from table 5 that only three of the broods consisted of more than one larva. The larvae could be segregated into two groups, red and pale orange.

The pale orange individuals have almost yellow spots just after the larva changes into its last instar and these become progressively more orange with age, suggesting the action of a rate gene.

In table 6, the colour of the spots of the full-grown larva has been given using the colour atlas of Villalobos and Villalobos (1947). It will be seen that the hue of individuals scored as red (or orange) always falls on pages 4 and 5, whereas it falls on page 6, 7 or 8 for those scored as pale orange. (The colour matching was done by Dr. A. J. Cain who did not

know how the larvae had been scored with regard to red and pale orange.) When the colour fell between two pages it was scored as the page nearest it in colour. In this connection it is interesting to note that the colour of no full-grown larvae fell between pages 5 and 6, although it did between other pages.

TABLE 6

mating	parents	colour atlas			number of larvae	scored
		hue page	degree	value		
19	16×16	4	12	14	1	R
		4	12	15	1	R
		5	11	14	1	R
		5	11	15	1	R
		5	12	13	1	R
		5	12	14	1	R
		5	12	15	7	R
		5	12	16	6	R
		—	—	—	2	R
		6	11	16	2	P.O.
		6	12	16	2	P.O.
		6	12	17	1	P.O.
		7	11	17	1	P.O.
		7	12	17	3	P.O.
		—	—	—	2	P.O.
20	16×16	4	11	14	1	R
		4	12	14	2	R
		5	12	15	3	R
		5	12	16	1	R
		—	—	—	1	R
		7	12	17	1	P.O.
		8	12	17	3	P.O.
a	16×16	5	12	14	1	R
		5	12	15	3	R
		—	—	—	1	R
		7	12	17	1	P.O.
47	19×19	4	12	13	2	R
		4	12	14	3	R
		4	12	15	1	R
		5	12	14	5	R
		5	12	15	1	R
		5	12	16	1	R
		6	12	16	2	P.O.
		6	12	17	1	P.O.
		7	12	17	2	P.O.
36	19×19	6	12	15	8	P.O.
		6	12	16	14	P.O.
		6	12	17	2	P.O.
		7	12	15	1	P.O.
		7	12	17	8	P.O.
		10	11	17	1	Y
		10	12	17	2	Y
		10	12	18	8	Y
		10	12	19	1	Y
		11	12	17	1	Y
		11	12	18	1	Y

It is clear that more than one gene is affecting the segregation for larval spot colour. One of the original parents had a red spotted larva, the other a yellow one, but in the first generation in which segregation occurred it was for red and pale orange, instead of red and yellow, in a ratio not significantly different from 3 : 1. Moreover, the results cannot be explained by assuming that the pale orange individuals are the result of some heterozygotes manifesting their effects, for the adults of two larvae which had pale orange spots when mated produced only pale orange and yellow individuals in the ratio of about 3 : 1. In view of the fact that the three classes seem to be distinct, it is probable that major genes are involved and that there are at least two of these concerned. Appropriate matings have been made to elucidate the genetics of the situation. In the only one to yield results so far (a backcross of the F.1 hybrid to *P. p. asterius*) there was an apparent 1 : 1 segregation of 9 yellow to 9 orange or red spotted larvae. This shows that the recessive gene producing yellow converts red, orange, and pale orange to yellow. However, too few larvae reached maturity, because of virus disease, for it to be possible to decide if there is a second major gene converting red into pale orange, or whether this change is controlled by many genes. Moreover, the situation is clearly complex, for evidence is accumulating that the degree of dominance of red over yellow varies from one subspecies of *P. machaon* to another. In some matings the F.1 hybrids are similar to *P. machaon* larvae in colour while in others they are pale orange.

It must be borne in mind that the original parents were very distinct genetically so that the segregation may be the result of whole chromosomes failing to pair at meiosis but the results are too regular for this explanation to be likely. There is also the possibility that it is only apparent, because the intermediate forms are less viable and therefore do not appear among the full-grown larvae. Against this is the fact that in Mating 19 only nine eggs failed to hatch and of the forty-two that did hatch, thirty-two reached a sufficiently large size to allow them to be scored for spot colour, suggesting that there was no very heavy selective elimination of intermediate types.

Eye-spot on the Anal Angle of the Hind-Wing

The eye-spot is very similar in *P. p. asterius*, *P. brevicauda* and *P. zelicaon* and drawings of the spot of *P. p. asterius* are given in figure 1A, 3 and figure 2. *P. machaon* differs from these species in several respects. The area of red scales tends to be larger than in the preceding three species, there is no black central pupil, instead the red area is bordered by a curved posterior line of black and at the anterior end of the red area there is a region which has blue scales present as

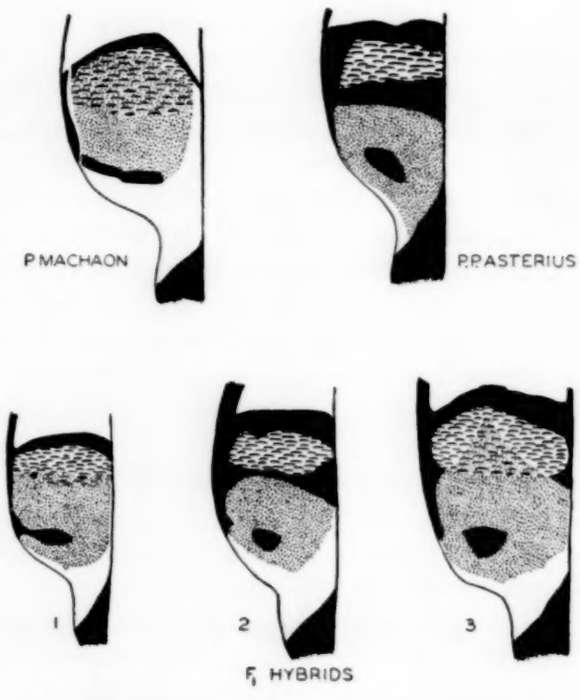

FIG. 2. Parent specimens of *P. machaon* and *P. p. asterius* together with three of their offspring, chosen to indicate the range of variability in the shape of the pupil in the F.1 generation. The examples are taken from Mating 9. (1) and (3) are the two extremes and (2) shows the mode for the ratio of the lengths *ef/gh*. Note also the variability in the ratio of the lengths, *cd/bc*.

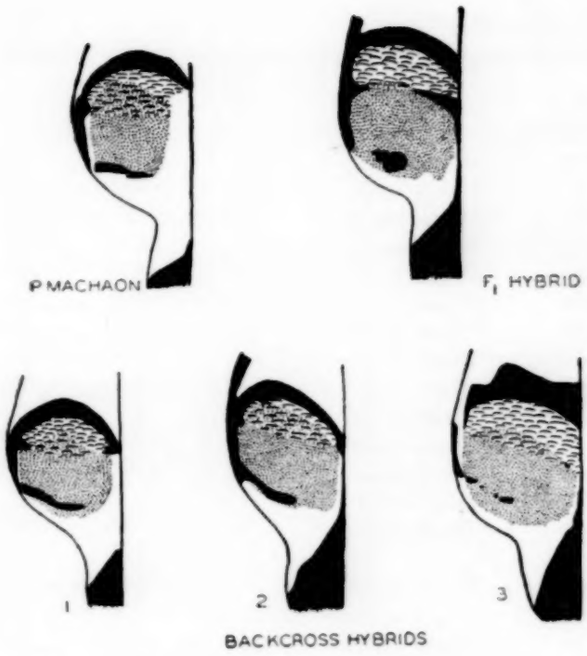

FIG. 3. Parents of Mating 16, together with three of their offspring, chosen in the same way as those for figure 2. Note how, as the result of this backcross to *P. machaon*, both the pupil and the ratio of the depth of the black area to the red have become more machaon-like, but are still very variable.

well as red ones. This red and blue area in *P. machaon* is bordered anteriorly by a black line of scales which is sometimes sufficiently broad to have some blue ones on it. This black line corresponds with the anterior black area in *P. p. asterius*, *P. brevicauda* and *P. zelicaon* (fig. 1A). It will be seen therefore that the eye-spot can differ in at least two distinct ways.

(1) The presence of either a black pupil or a black line in the eye-spot.

(2) The presence or absence of an area with both red and blue scales (fig. 1A).

The actual points on the eye-spot between which measurements have been taken are given above (pp. 182 and 183). The data on the measurements are too numerous to be given in full, but those for two of the species, *P. machaon* and *P. p. asterius*, together with some of their hybrids (see figs. 2 and 3), are given in tables 7, 8 and 9.

The characteristic features distinguishing the North American species from the European *P. machaon* are the shape of the pupil and the ratio of the depth of the black to the red area. In order to get a measurement of the difference in the shape of the pupil the ratio *ef/gh* (see fig. 1) has been calculated. This removes complications due to the varying absolute size of the eye-spots (except any due to allometric growth). For the second character, the ratio *cd/bc* has been calculated. Both these will distinguish *P. machaon* from the other three species. In figures 4 and 5 these ratios are plotted in the form of histograms for *P. p. asterius*, *P. machaon*, the F.1 hybrid between them (Mating 9), the backcross of the F.1 hy-

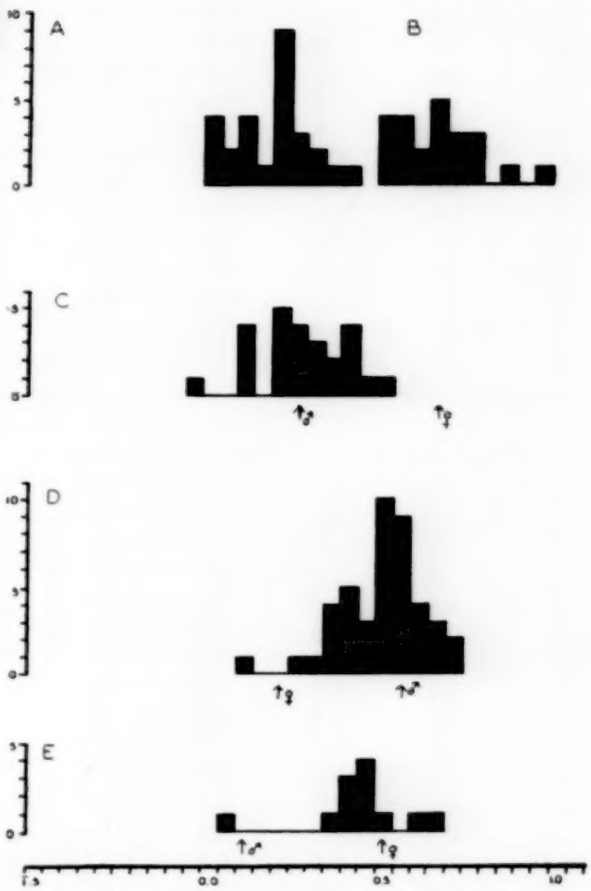

FIG. 4. Values of the ratio *ef/gh* for a number of (A) *P. p. asterius*, (B) *P. machaon*, (C) their F.1 hybrid (Mating 9), (D) one of the hybrids backcrossed to *P. machaon* (Mating 16), and (E) one of the latter brood backcrossed to *P. p. asterius* (Mating 35). The ratio has been transformed to logarithms to make the variability, in the various histograms, more comparable. Arrows indicate the ratio for the pupil of the parents of the brood against which the arrow is placed.

TABLE 7. *P. p. asterius*

ef	*gh*	$\frac{ef}{gh}$	*bc*	*cd*	$\frac{cd}{bc}$		
1.4	0.8	1.8	2.5	1.9	0.76	Black male	
1.5	1.0	1.5	2.4	2.6	1.1	Black male	
2.2	1.2	1.8	3.5	2.9	0.83	Black male	Parent of mating 9
1.7	0.9	1.9	3.9	2.6	0.67	Black male	
1.5	1.2	1.2	3.6	3.0	0.83	Black male	
2.4	1.1	2.2	2.5	2.0	0.80	Black male	
1.9	1.2	1.6	2.8	1.9	0.68	Black male	
1.1	1.0	1.1	2.6	2.5	0.96	Black male	
0.8	0.6	1.3	1.6	2.2	1.4	Black male	Parent of mating 35
2.2	1.4	1.6	4.0	3.0	0.75	Black male	
1.6	1.2	1.3	2.7	2.4	0.89	Black male	
1.0	1.0	1.0	3.1	2.5	0.81	Black male	
1.6	1.0	1.6	3.2	2.2	0.69	Black male	
2.3	1.9	1.2	3.5	2.4	0.69	Black male	
2.3	1.4	1.6	3.6	2.5	0.69	Black female	Parent of mating 1
1.9	1.2	1.6	3.5	3.2	0.91	Black female	
0.6	0.6	1.0	1.8	2.3	1.3	Black female	
2.4	1.5	1.6	4.0	3.5	0.88	Black female	
2.5	1.7	1.5	3.1	3.4	1.1	Black female	
3.1	1.9	1.6	4.0	3.2	0.80	Black female	
2.1	1.9	1.1	4.0	3.5	0.88	Black female	
3.8	1.8	2.1	4.0	3.5	0.88	Black female	
2.4	1.0	2.4	2.9	2.0	0.69	Black female	
1.6	0.9	1.8	4.2	2.3	0.55	Black female	
1.2	1.2	1.0	3.6	2.8	0.78	Black female	
1.6	1.6	1.0	2.8	3.5	1.2	Black female	
2.0	1.2	1.7	3.0	2.4	0.80	Black female	
				P. machaon			
2.6	0.8	3.2	1.4	3.9	2.8	Yellow male	
3.2	0.9	3.6	1.5	3.6	2.4	Yellow male	
2.9	0.8	3.6	1.9	5.6	2.9	Yellow male	
2.5	0.8	3.1	0.9	4.1	4.6	Yellow male	
3.2	0.8	4.0	1.8	4.5	2.5	Yellow male	
2.4	0.8	3.0	1.2	4.2	3.5	Yellow male	
2.6	0.8	3.2	1.2	4.5	3.8	Yellow male	
2.2	0.6	3.7	1.2	3.4	2.8	Yellow male	
2.4	0.7	3.4	1.2	3.6	3.0	Yellow male	Parent of mating 16
3.3	0.7	4.7	1.2	3.9	3.2	Yellow male	
2.7	0.3	9.0	0.6	3.6	6.0	Yellow male	Parent of mating 44
2.8	0.5	5.6	0.5	4.1	8.2	Yellow male	
2.4	0.5	4.8	0.7	4.3	6.2	Yellow male	Parent of mating 45
2.9	0.5	5.8	0.8	3.7	4.6	Yellow male	Parent of mating 38
2.7	0.6	4.5	1.4	3.8	2.7	Yellow male	
3.6	0.5	7.2	1.2	4.5	3.8	Yellow male	
2.5	0.5	5.0	0.6	3.2	5.3	Yellow male	
2.6	0.6	4.3	1.6	4.0	2.5	Yellow male	
4.0	0.8	5.0	1.0	4.0	4.0	Yellow male	
3.4	0.8	4.2	0.7	4.9	7.0	Yellow female	Parent of mating 9
3.2	0.6	5.3	1.0	3.7	3.7	Yellow female	
3.5	0.8	4.4	1.5	3.9	2.6	Yellow female	Parent of mating 23
3.7	0.9	4.1	0.8	5.1	6.4	Yellow female	

TABLE 8. *Mating 9 (a♂ × m♀)*

ef	*gh*	$\frac{ef}{gh}$	*bc*	*cd*	$\frac{cd}{bc}$		
1.6	0.8	2.0	2.4	3.2	1.3	Black male	
1.8	0.8	2.2	2.4	3.9	1.6	Black male	
1.8	1.1	1.6	2.2	3.4	1.5	Black male	
1.0	0.6	1.7	1.7	3.3	1.9	Black male	
0.6	0.4	1.5	3.0	2.8	0.93	Black male	
1.6	0.8	2.0	2.6	2.7	1.0	Black male	
2.6	1.2	2.2	2.6	3.2	1.2	Black male	
2.5	1.0	2.5	2.2	3.6	1.6	Black male	
2.3	0.9	2.6	2.3	3.0	1.3	Black male	
1.3	1.0	1.3	2.9	3.4	1.2	Black male	
1.0	0.6	1.7	2.6	2.9	1.1	Black male	
2.7	1.0	2.7	2.4	3.5	1.5	Black male	
2.4	1.0	2.4	2.2	4.0	1.8	Black female	
1.9	1.1	1.7	2.3	3.8	1.7	Black female	
3.0	1.2	2.5	2.4	2.4	1.0	Black female	
1.4	1.1	1.3	2.1	4.1	2.0	Black female	
1.2	0.9	1.3	2.1	4.5	2.1	Black female	
1.2	0.7	1.7	1.6	4.6	2.9	Black female	
2.4	0.8	3.0	1.4	3.5	2.5	Black female	
1.1	0.6	1.8	2.5	4.1	1.6	Black female	
1.6	1.8	0.89	1.7	5.8	3.4	Black female	
1.4	0.9	1.6	2.3	3.5	1.5	Black female	Parent of mating 16
1.8	1.4	1.3	2.5	4.6	1.8	Black female	
1.3	0.7	1.9	1.4	3.5	2.5	Black female	
1.4	0.7	2.0	1.5	3.8	2.5	Black female	
				Mating 35 (16♀ × a♂)			
3.0	0.7	4.3	3.1	2.5	0.81	Black male	
2.2	0.8	2.8	2.2	3.0	1.4	Black male	
1.9	0.5	3.8	3.4	2.0	0.59	Black male	
2.8	1.0	2.8	2.6	2.6	1.0	Black male	
1.4	1.3	1.1	2.2	2.8	1.3	Black male	
2.6	1.2	2.2	2.5	2.6	1.0	Black male	
2.3	0.9	2.6	2.4	2.3	0.96	Black male	
2.8	1.0	2.8	2.4	2.7	1.1	Black male	
2.6	0.8	3.2	2.2	2.3	1.0	Black male	
2.8	1.0	2.8	2.5	2.8	1.1	Black male	
2.6	1.0	2.6	3.0	3.1	1.0	Black female	
2.3	0.9	2.6	4.0	3.0	0.75	Black female	

brid to *P. machaon* (Mating 16) and for a female of this last brood crossed to *P. p. asterius* (Mating 35). The ratios have been transformed into logarithms, before they were plotted, in order to make the variability in the different groups more nearly comparable. The variability in the measurements and ratios, the lack of more discontinuities in the backcross families than in the parents and F.1, and the failure to recover in the backcross families the full range of parental and F.1 variation strongly argue in favour of a complex genetical control of these differences between *P. machaon* and *P. p. asterius*. Other data show that the same is true for *P. machaon* and *P. brevicauda* and also probably *P. zelicaon*. The absence of a marked correlation between the two ratios in the individuals indicates

that, in the main, different genes are controlling the two characters.

The Inheritance of Orange in the Sub-marginal lunules

The four sub-marginal lunules are orange in *P. p. asterius* and yellow in *P. machaon*. The F.1 hybrids are intermediate and when these are backcrossed to *P. machaon*, all or very nearly all of the orange disappears, nor has it reappeared to any extent among sib matings of the offspring of this backcross. If the presence of orange were controlled by a single gene, then after a backcross to *P. machaon*, half the offspring should be like the F.1 in appearance. Since this is not so, it is probable that the character is controlled by several genes.

TABLE 9. *Mating 16* (9 ♀ × *m* ♂)

ef	*gh*	$\frac{ef}{gh}$	*bc*	*cd*	$\frac{cd}{bc}$		
2.4	0.9	2.7	1.6	3.8	2.4	Black male	
2.5	0.6	4.2	1.8	3.5	1.9	Black male	
2.4	1.1	2.2	1.1	3.5	3.2	Black male	
2.4	0.6	4.0	0.9	3.4	3.8	Black male	
2.0	0.8	2.5	1.8	2.9	1.6	Black male	
1.9	0.6	3.2	1.2	3.7	3.1	Black male	
2.4	1.0	2.4	1.3	4.0	3.1	Black male	
2.0	0.8	2.5	1.6	3.8	2.4	Black male	
1.8	0.8	2.2	1.8	3.4	1.9	Black male	
2.2	0.7	3.1	2.1	2.6	1.2	Black male	
1.8	0.7	2.6	1.4	3.1	2.2	Black male	
2.1	0.6	3.5	1.1	3.5	3.2	Black male	
2.2	0.7	3.1	1.2	3.9	3.2	Black male	
2.6	0.6	4.3	1.7	2.8	1.6	Black male	
1.8	0.8	2.2	0.9	3.8	4.2	Black male	
1.6	0.9	1.8	0.9	3.6	4.0	Yellow male	
2.1	0.6	3.5	1.7	3.1	1.8	Yellow male	
2.1	0.6	3.5	1.9	2.6	1.4	Yellow male	
1.4	0.4	3.5	1.1	3.6	3.3	Yellow male	
2.8	0.7	4.0	1.7	3.9	2.3	Yellow male	
2.1	0.4	5.2	1.3	3.2	2.5	Yellow male	
1.9	0.8	2.4	1.2	3.8	3.2	Yellow male	
2.5	0.8	3.1	1.1	4.3	3.9	Yellow male	
0.5	0.4	1.2	2.4	3.5	1.5	Yellow male	
3.0	1.0	3.0	1.5	4.5	3.0	Black female	Parent of mating 35
2.3	0.8	2.9	1.3	3.5	2.7	Black female	
3.4	1.2	2.8	1.8	3.9	2.2	Black female	
3.6	1.2	3.0	2.9	3.8	1.3	Black female	
2.6	0.6	4.3	1.4	4.1	2.9	Black female	
3.1	0.8	3.9	1.1	5.0	4.5	Black female	
3.2	1.0	3.2	2.1	4.6	2.2	Black female	
1.4	0.7	2.0	1.6	4.5	2.8	Yellow female	
3.2	0.9	3.6	2.3	3.8	1.7	Yellow female	
2.6	0.7	3.7	2.6	4.1	1.6	Yellow female	
2.7	0.6	4.5	2.5	3.1	1.2	Yellow female	
3.0	0.8	3.8	1.0	5.1	5.1	Yellow female	
2.8	0.9	3.1	1.1	4.9	4.5	Yellow female	
2.8	0.8	3.5	1.1	5.8	5.3	Yellow female	
2.1	0.9	2.3	0.9	4.5	5.0	Yellow female	
2.8	0.8	3.5	1.4	3.8	2.7	Yellow female	
2.6	0.8	3.2	0.8	4.9	6.1	Yellow female	
2.6	0.5	5.2	1.5	4.8	3.2	Yellow female	
2.9	0.9	3.2	1.2	6.5	5.4	Yellow female	

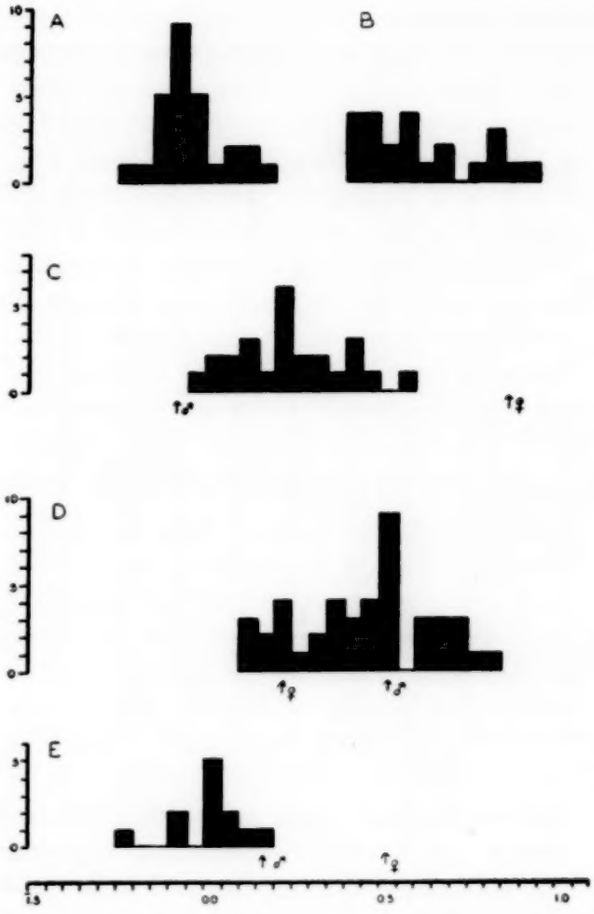

FIG. 5. The histograms are constructed in the same way and using the same individuals as those in figure 4, except that here the values of the ratio *cd/bc* have been plotted.

The inheritance of Yellow on the Legs and Yellow Scaling on the Underside at the Apex of the Fore-wings

The single dominant gene controlling the black ground-colour of the wings also controls the colour of the body. Moreover, in the presence of this gene, the femur of the leg is black; in its absence it is partially yellow, unless other genes are present which give a black femur as in some *P. zelicaon*. The yellow smudge (p. 184) and partly yellow tibia of *P. machaon* appear in hybrids between it and *P. p. asterius* or *P. brevicauda* where the yellow is absent. The presence of yellow in these two areas is independent of the dominant gene *B*, although it is not yet known whether its presence in one of these areas is independent of its presence in the other. It was provisionally suggested (Clarke and Sheppard, 1953) that the presence or absence of the marked apical smudge and the yellow on the legs might be controlled by the gene *B*. However, this is not so, although it is true to say that the amount of yellow on the legs is in part controlled by it, as the femur is black in the presence of that gene. The independence of the yellow smudge and yellow tibia from the gene *B* can be seen in Mating 19 and 35 (tables 2 and 4). These matings produced some homozygous black individuals, yet all had a yellow apical smudge (although it varied in expression), and all had yellow on the tibia of the leg in Mating 19 but not in 35. It is interesting to note that *P. zelicaon*, although it has yellow ground-colour on the wings, has black or nearly black legs and a less marked apical smudge than is found in *P. machaon*. As a consequence of this, the hybrid between it and *P. p. asterius* has black legs and either no yellow smudge or a reduced one; that is to say, *P. zelicaon* differs from *P. machaon* in respect of these genes.

The Inheritance of Black and Yellow in the "Cell" on the Underside of the Fore-wing

The three American species have a black "cell" whereas *P. machaon* has one which is mostly yellow. Among hybrids between *P. machaon* and *P. p. asterius* or *P. brevicauda* backcrossed to *P. machaon* all the yellow individuals have a yellow "cell" whereas the black butterflies have a black "cell," showing that in the presence of the gene for black *B* the "cell" is black. However, in *P. zelicaon* which is yellow the "cell" is black. Moreover, hybrids between *P. machaon* and *P. zelicaon* have a black "cell" and the only individual obtained by backcrossing one of these hybrids to *P. machaon* had a yellow one. This character is inherited but it is not clear whether it is multifactorial or not, although several genes are probably involved as different individuals of *P. machaon* vary slightly with regard to this

TABLE 10. *Fertility of matings*

Mating	Parents female	Parents male	Genotypes or phenotypes	Infertile	Started to develop	Fully-formed larva	Hatched	Total	Matings with no eggs
9	m	a	bb×BB	3	0	2	52	57	
16	9	m	Bb× bb	5	0	0	90	95	
17	9	m	Bb× bb	2	0	28	45	75	
18	9	m	Bb× bb	2	0	21	64	87	
—	9	m	Bb× bb	8	0	0	0	8	
—	m	9	bb× Bb	25	1	0	0	26	
—	9	9	Bb× Bb	5	0	0	0	5	
—	9	9	Bb× Bb	35	0	0	0	35	
—	9	9	Bb× Bb	6	0	0	0	6	
—	9	9	Bb× Bb	29	0	0	0	29	
—	9	9	Bb× Bb	68	0	0	0	68	
—	9	10	Bb× Bb	8	0	0	0	8	
—	9	10	Bb× Bb	23	0	0	0	23	
19	16	16	Bb× Bb	0	1	8	42	51	
—	16	16	Bb× Bb	1	0	0	0	1	
—	16	16	Bb× Bb	33	0	0	0	33	
—	16	16	Bb× Bb	35	0	0	0	35	
—	16	16	bb× Bb	9	0	0	0	9	
—	16	16	bb× Bb	4	1	1	6	12	
—	16	16	bb× Bb	0	0	0	0	0	2
—	16	16	Bb× bb	55	9	4	10	78	
—	16	16	Bb× bb	0	0	0	0	0	1
—	16	16	bb× bb	0	3	0	0	3	
—	16	16	bb× bb	32	9	7	8	56	
20	16	16	bb× bb	21	10	11	19	61	
—	16	16	bb× bb	0	0	0	0	0	2
—	16	m	Bb× bb	5	0	0	0	5	
—	16	m	Bb× bb	0	0	0	0	0	3
—	16	a	bb×BB	6	0	0	0	6	
—	16	a	bb×BB	26	0	0	0	26	
—	16	a	bb×BB	5	0	0	0	5	
35	16	a	Bb×BB	10	23	15	26	74	
—	16	a	Bb×BB	54	0	0	0	54	
—	17	17	Bb× bb	6	0	0	0	6	
—	17	17	Bb× Bb	4	0	0	0	4	
—	17	17	bb× Bb	20	1	3	0	24	
44	17	m	Bb× bb	30	6	0	28	64	
45	17	m	Bb× bb	16	1	3	9	29	
—	17	m	bb× bb	0	0	0	0	0	1
—	18	18	bb× bb	1	0	0	0	1	
—	18	18	bb× Bb	5	0	0	0	5	
—	18	20	bb× bb	1	0	0	0	1	
—	18	20	bb× bb	0	0	0	0	0	1
—	19	16	B× Bb	1	0	0	0	1	
—	19	16	B× Bb	12	0	0	0	12	
—	19	16	B× Bb	48	0	0	0	48	
—	19	19	B× B	28	0	0	0	28	
—	19	19	B× B	1	0	0	0	1	
48	19	19	Bb× Bb	8	30	14	67	119	
47	19	19	Bb× Bb	8	25	2	50	85	
—	20	20	bb× bb	0	0	0	0	0	1
46	45	45	Bb× bb	0	0	0	44	44	

character. It is also not known whether the gene or genes controlling this character are the same as those effecting the amount of black on the legs, nor is the genotype of *P. p. asterius* and *P. brevicauda* known in respect of these genes.

Fertility

Not once has a fertile mating been obtained between sibs of any F.1 hybrid so far produced, despite the fact that many such matings have been obtained and that some of the females have laid considerable numbers of eggs. Only backcrosses of hybrids to one or other of the parent species have produced any fertile eggs and even then the matings have often proved partly or completely infertile. The data on infertility and poor viability are now too great to be dealt with in full here. However, in table 10 will be found a complete record of the matings obtained among one family derived from a cross between *P. machaon* and *P. p. asterius*. The data give the number of eggs laid, the number that started to develop as judged by changing colour (this usually occurs in two or three days at 70° F.), the number of eggs with fully formed larvae within them which fail to hatch (at this stage the egg turns black), and the number that hatched. No account of the number surviving at later stages has been given, as this is very much affected by the presence or absence of virus disease. If there is no virus disease a large proportion of the larvae pupate successfully, although there are suggestions of a rather high mortality among the pupae in some hybrid broods.

After one backcross the fertility of sib matings between hybrids is much improved (table 10), and there seems to be no relationship between the genotype with respect to *B* and *b* and infertility. Part of the failure of eggs to hatch is due to irregularities in development, but it is not certain whether some is not due to the absence of fertilization. That this may be so is suggested by the tendency for the number of eggs in a brood in which no sign of development is seen in any egg to be smaller than in broods where a large proportion of the eggs start to develop. There is also a tendency for females of hybrid origin which lay no fertile eggs to

start to lay later in life than those which produce some fertile eggs. The two tendencies have also been noted when both parents have been of the same species and therefore where failure to develop is probably due to the absence of fertilization. The data suggest that meiosis in hybrids is not more abnormal in one sex than the other as both sexes of the hybrids can be fertile, that many genes affect their fertility and that there can be little genetic interchange between the species in the wild.

Single Broodedness

P. *brevicauda* is single brooded in its native haunts (McDunnough, 1939) whereas *P. p. asterius* and *P. machaon* are at least partially double brooded over much of their range and even triple brooded in some areas. It will be noticed from tables 2, 3 and 4 that when some pupae remain from a brood long after the others have emerged, *P. brevicauda* is nearly always one of the ancestors. As all the broods were kept in similar conditions, this suggests rather strongly that the single broodedness of *P. brevicauda* is inherited and is not just the result of the environment in which it lives. However, the environment has no doubt caused selection for single broodedness.

Discussion

Fisher (1930) has shown that the greater the effect of a mutant, the more likely it is to be deleterious and therefore to fail to spread in a species. Consequently most of the genetic differences between species should involve genes having small effects (polymorphism excepted) and this has been found to be true in the present investigation. However, this does not mean to say that all sharply contrasting characters by which species are identified will necessarily be multifactorially controlled. By definition, major genes will produce easily recognized effects and therefore whenever there is a major gene difference involving structure, the character it controls is likely to be one of those by which the species is distinguished. It is therefore possible that some, although not all, the striking differences distinguishing species, may be controlled by single genes, but that the species will also differ by very many others having much smaller effects. In the aggregate, these minor genes may be much more important in determining the absence or extent of genetic interchange between the forms, for example by determining the infertility of the hybrids.

The genetic differences between the

Table 11

	1 ground-colour		2 sexual dimorphism	3 yellow apical smudge	4 yellow on legs		5 yellow "cell"	6 eye spot		7 orange lunules	8 red larval spots	
		area of black*	*		femur**	tibia	**	pupil	broad anterior border			†
P. machaon	*bb*	+	+	++	+	++	+	−	−	−	*YY*	+
P. zelicaon	*bb*	+	+	+	−	+	−	+	+	−	*YY*, *Yy* or *yy*	?
P. p. asterius	*BB*	−	++	−	?	−	?	+	+	+	*yy*	−
P. brevicauda	*BB*	−	−	−	?	−	?	+	+	+	*yy*	?

B and *b* refer to the pair of allelomorphs controlling ground-colour. *Y* and *y* refer to the allelomorphs controlling larval spot colour with respect to red and yellow. + and the more extreme ++ indicate the presence of several genes increasing the expression of the character at the head of the column, and − the presence of genes not producing or increasing the expression of the character. * indicates that the genes listed in the column only manifest their expression in the presence of the allelomorph *B*, ** only in its absence and † indicates that they only express themselves in the presence of the allelomorph *Y*.

species are summarized in table 11 and by comparing this with table 1, it is possible to see that the main differences between *P. machaon* and *P. zelicaon* are controlled multifactorially. Those distinguishing *P. p. asterius* and *P. brevicauda* are also multifactorial except for one of the main differences, the presence or absence of marked sexual dimorphism in wing pattern, which may involve a major gene with modifiers (the genetics of the character short tails in *P. brevicauda* has not yet been investigated adequately, nor has the difference in the shade of yellow on the yellow bands in *P. p. asterius* and *P. brevicauda*).

Unfortunately table 11 is somewhat arbitrary since it is assumed that similar characters are controlled by the same genes, nor does the table give due weight to the number of genes involved in the production of multifactorially controlled characters. However, it indicates in a rather more precise way than the mere description of characters, how the species have diverged genetically, since it makes a distinction between, for example, the absence of sexual dimorphism in *P. machaon* on the one hand, and in *P. brevicauda* on the other. The data agree with predictions based on mathematical theory, in that most of the differences are multifactorial, and no doubt if the forms continue to diverge, a larger and larger proportion of the striking differences between them will be controlled multifactorially, although the actual number of major gene differences may also increase.

If the time at which the various forms originally became isolated could be established, it would be possible to get a good estimate of the speed at which divergence had occurred in terms of genetic differences, which would be valuable in the study of evolution. The distribution of the four forms that have been studied suggests that they were isolated from each other during the Pleistocene, particularly *P. brevicauda* and *P. p. asterius*. However, there is still the possibility that they had been isolated at an earlier period as well. Only a very close study of the distribution of these forms with respect to one another, as well as their ecology and their relationship to other forms of the Machaon-group in North America, could enable one to decide when they were isolated from one another.

These other members of the North American group include *P. indra* Reak., *P. nitra* Edw. and a complex of forms, *bairdi* Edw., *oregonia* Edw., *brucei* Edw. and *hollandi* Edw., which are all probably very closely related. *P. indra* differs from all the other forms so far mentioned in this paper, in that its genitalia can easily be distinguished from those of the others. This form has a black ground-colour and no marked sexual dimorphism and has evolved two distinct subspecies. It seems probable that it has been isolated from the others longer than they have been from each other. *P. nitra* is a local and uncommon butterfly, found in an area where *P. machaon* and *P. p. asterius* overlap. It is very like the hybrid between these two species in all respects, except that it is not sexually dimorphic (Rothschild and Jordan, 1906). If this is a hybrid, which seems very likely, then it is probable that not all North American *P. machaon* are genetically sexually dimorphic as apparently are those from Europe and Japan. This can only be tested when living *P. machaon* can be obtained from an area where *P. nitra* is found.

The other interesting group of forms comprises *bairdi, oregonia, brucei* and *hollandi*. All are found flying together in some areas and it seems probable that all interbreed. *Oregonia* is a large insect with a yellow ground-colour and is almost indistinguishable from the yellow insects produced by mating *P. machaon* with *P. p. asterius* and backcrossing to *P. machaon*. It is very variable in the shape of the pupil of the eye-spot, as was pointed out by Hagen (1882) and Edwards (1883). It or yellow forms like it are found from British Columbia in the north to Colorado and Arizona in the south.

In Colorado and Arizona there is another form, *bairdi*, which Edwards (1893, 1895 and 1898) has investigated genetically. He showed (without, of course, realizing it) that the difference between the yellow forms and *bairdi* is due to a dominant gene producing a black ground-colour on the wings. This is, almost certainly, the same gene *B* which distinguishes *P. p. asterius* and *P. brevicauda* from *P. machaon* and *P. zelicaon*. In Arizona the yellow forms are rare compared with *bairdi* and their presence was unknown to Edwards (1895).

Both *oregonia* and *bairdi* are so like the hybrids that have been obtained using *P. p. asterius* and *P. machaon* that at first sight, they appear to constitute a hybrid zone. However, *P. machaon* has not extended its range far enough south to be involved, except perhaps in Canada. Moreover the pupil of the eye-spot is clearly the wrong shape to be due to hybridization between *P. p. asterius* and *P. zelicaon*, as the hybrid has a round pupil. Consequently *oregonia* and *bairdi* may be yet another species or subspecies of the Machaon-group with a cline in the frequency of the yellow gene *b* from north to south. Whether this is a separate species can only be decided by genetic and ecological investigations. Edwards decided that it was on the grounds that the larva did not feed on the usual plants eaten by the Machaon-group (Umbelliferae), but fed on *Artemisia*. However, hybrids between *P. machaon* and *P. p. asterius* will also feed and lay eggs on it.

One other form which has not been investigated by us is the Central American, *P. americus*. This is polymorphic for a black ground-colour in at least one area (Rothschild and Jordan, 1906). The genetic analysis of this species will be of considerable interest.

It is clear that the Machaon-group provides some of the most suitable material ever investigated in animals for studying the process of speciation in detail, taking into account genetic, ecological and behaviour differences as well as time. Although a considerable amount of progress has been made in the course of a year's study, it is clear that, as well as a more detailed genetic investigation, a considerable amount of field work must be carried out. The type of work that is needed is well illustrated by the example of *P. p. asterius* and *P. brevicauda*. There is at least one locality where the two species fly together and hybrids from this colony have not been reported (McDunnough, 1939). It is possible that these have been overlooked, although it seems unlikely that they can be frequent. Only field observation can show whether the two forms remain distinct in this locality because of the hybrids being disadvantageous or because of the absence of mating between the species. This locality is also of interest as McDunnough (1939) reported that the larvae of both *P. brevicauda* and *P. p. asterius* from the colony have orange spots, which suggests that in some areas these two species may be polymorphic for the character, as is *P. zelicaon*, or that the orange genotype replaces the yellow one in some colonies.

Only an investigation into the amount of genetic interchange which takes place in the wild when the various forms are found flying together, can decide whether they should be called species or not. However, these forms do overlap with one another to some extent and the evidence on hybrid infertility alone suggests that there cannot be much genetic interchange between them and that they must be regarded as extreme subspecies at the very least.

The reduced fertility of the hybrids coupled with the variability in the degree of fertility and viability between the individuals indicates that many genes are involved in the genetics of this situation. Consequently both infertility and poor viability of hybrids can be evolved by a series of stages and do not require systemic mutations of the type postulated by Goldschmidt (1940). Goldschmidt (1940) defined the differences between species in an unrealistic way by making them qual-

itatively different by definition without indicating in any way the arbitrariness of the definition itself. He did not point out that the difference is only qualitative because the change from subspecific to specific rank is taken at that point when there ceases to be gene flow (or appreciable gene flow) between populations because of some barrier which is not spatial or temporal (for more detailed definitions see Cain, 1953; Mayr, 1942). Had he done so it would have been clear that species could evolve gradually from subspecies.

Summary

1. The present investigation has shown that the two black American swallowtails, *P. p. asterius* and *P. brevicauda,* differ from the two yellow ones, *P. zelicaon* and *P. machaon,* with respect to the black, by a single gene which is dominant to yellow. *P. machaon* has larvae with red spots, whereas those of *P. brevicauda* and *P. p. asterius* have yellow ones. This difference is also due to a single pair of allelomorphs with incomplete dominance. *P. zelicaon* is polymorphic for the character.

2. Ten other characters, by which some of the species differ from others, have been investigated. All these are controlled multifactorially. However, one may be under the control of a single major gene with modifiers. This is the presence or absence of a sexual dimorphism which only expresses itself among individuals with a black ground-colour. Both the yellow species as well as *P. p. asterius* have gene-complexes which produce sexual dimorphism in the presence of the dominant gene controlling black ground-colour, but, *P. brevicauda* does not.

3. All the F.1 hybrids which have been obtained have been infertile when mated with sibs. The backcrosses to the parent species have sometimes produced fertile eggs and sib-matings have been obtained after one backcross generation. The variability between individuals within a brood suggests that this character is controlled by many genes.

4. A number of other species closely related to *P. machaon* are found in North America. These have not yet been investigated genetically by us, but one, *P. bairdi,* is polymorphic for black ground-colour, controlled by a single dominant gene. This is almost certainly the same gene which distinguishes *P. machaon* from *P. p. asterius.*

5. Two species are known, therefore, each polymorphic for one of the two pairs of major genes controlling specific differences that have been identified. All the other species investigated are apparently monomorphic for one or other allelomorph at the two loci.

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MEASUREMENT OF GENE FREQUENCY DRIFT IN SMALL POPULATIONS[1]

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INTRODUCTION

The causes of changes in gene frequency from generation to generation in an evolving population may be thought of as being of two kinds (Wright, 1949, 1951): (1) systematic factors (selection, mutation, and migration) which tend to carry the gene frequency to an equilibrium point, and (2) dispersive factors (chance fluctuations in finite populations and variations in the magnitude and direction of the systematic factors) which cause the gene frequency to scatter. The result of these two factors is a stochastic process leading to a succession of changes in gene frequency. The mathematical formulation of this process and the distribution of gene frequency probabilities when a steady state is reached have been the subject of much mathematical inquiry (Fisher, 1922, 1930; Wright, 1931, 1945, 1949, 1952; Kolmogoroff, 1935; Malecot, 1948; Feller, 1951; Kimura, 1954). Wright and others have shown, by various methods, that the process is adequately described by the Fokker-Planck equation

$$\frac{\partial \phi(q, t)}{\partial t} = \frac{1}{2}\frac{\partial^2}{\partial q^2}[V_{\delta q}\phi(q, t)] - \frac{\partial}{\partial q}[M_{\delta q}\phi(q, t)] \quad (1)$$

where q is the frequency of the allele under consideration, t is time (measured in generations), $M_{\delta q}$ is the mean change in gene frequency per generation due to systematic factors, $V_{\delta q}$ is the variance in gene frequency change in one generation due to dispersive factors and $\phi(q, t)$ is the frequency function of the gene frequency. Feller (1951) has shown that the Fokker-Planck equation is valid under the most general conditions so that the only measurements needed for a specification of the process are the mean systematic increment, $M_{\delta q}$, and the mean square change due to dispersive factors, $V_{\delta q}$.

The mean systematic change in gene frequency per generation is determined completely in principle by mutation, migration, and selection rates. The most inclusive expression for this is Wright's Δq_e (1949, p. 378) which takes into consideration mutation among a series of alleles, migration among subgroups of a population, and selection including variable genotypic selective values.

That part of $V_{\delta q}$ which is due to sampling variance in a finite population is usually taken as the binomial value, $q(1 - q)/2N_e$ where N_e is the effective population number. This is equal to the actual number of breeding adults only in an idealized population in which a random gamete has an equal probability of having come from any parent. In nature the effective number would ordinarily be less than the actual number. The frequency of allelism of lethals has been used to estimate the effective number in natural populations of Drosophila (Dobzhansky and Wright, 1941) and in irradiated population cages (Prout, 1954). Kerr and Wright (1954) have determined the effective number from rate of fixation in very small laboratory populations.

Such studies are possible only in an organism such as Drosophila where usable mutants and the genetic techniques

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for detecting and maintaining lethals are available. The purpose of this inquiry was to find an expression for $V_{\delta q}$, and for the effective population number, in terms of quantities that are, at least in principle, capable of measurement by direct census methods and to make such measurements in a laboratory population of Drosophila.

Measurement of Effective Population Number

In order to determine the effective population number one needs to know (1) the number of reproducing adults, (2) the extent of non-random mating, and (3) the distribution of the number of surviving progeny per parent. We shall show in the next section that, in fact, only the mean and variance of the progeny distribution are needed.

The random drift in gene frequency in a population of effective size N_e will have a variance $q(1 - q)/2N_e$, where q is the frequency of the allele under discussion. The effective number for a non-ideal population may be defined by the relation $q(1 - q)/2N_e = V_{\delta q}$. As will be shown in the next section, for a population of randomly mating monoecious diploids,

$$V_{\delta q} = \frac{q(1-q)}{4N} \times \left[1 - F' + (1 + F')\frac{V_k}{\mu_k}\right] \quad (2)$$

where N is the total number of offspring, μ_k and V_k are the mean and variance of the number of surviving offspring per parent, and F′ is Wright's coefficient of inbreeding, used as a measure of the departure from random-mating zygotic proportions among the parents. The effective number, then, is

$$N_e = \frac{2N}{1 - F' + (1 + F')V_k/\mu_k}. \quad (3)$$

Derivation of Formulae for $V_{\delta q}$

Monoecious Diploids, Random Mating

We start with a parent population of N′ individuals, of which a proportion P are AA, Q are AA', and R are $A'A'$, where A is the allele under consideration and A' stands for all other alleles at this locus. Due to sampling accidents and variable numbers of progeny the proportion of A genes will be different in the next generation. The problem is to obtain the variance of this difference. A direct derivation is possible, but is long and tedious while a simple artifice makes possible a short, though indirect demonstration. (We shall be happy to send the longer derivation to any interested reader.)

Assume that N′ parents are chosen at random from a pool of gene pairs in which the proportions of AA, AA', and $A'A'$ are P, Q, and R respectively. The expected number of A genes per individual is 2q, where q is the proportion of A genes in the pool. The variance in the number of A genes in the N′ parents is given by

$$N'\{P(2 - 2q)^2 + Q(1 - 2q)^2 + R(0 - 2q)^2\}.$$

It is convenient to express the genotype frequencies in terms of gene frequencies and inbreeding coefficient F′, as follows

$$P = q^2(1 - F') + qF',$$
$$Q = 2q(1 - q)(1 - F'),$$
$$\text{and } R = (1-q)^2(1-F') + (1-q)F'. \quad (4)$$

Making these substitutions and dividing by the square of the total number of genes, $(2N')^2$, to obtain the variance in the *proportion* of A genes we obtain

$$\frac{q(1-q)}{2N'}(1 + F'). \quad (5)$$

Now assume that the ith parent contributes k_i genes to the offspring generation. The variance in the number of A

genes in the offspring is given by

$$\sum_{i=1}^{N'} \{P(k_i - qk_i)^2 + Q(\tfrac{1}{2}k_i - qk_i)^2 + R(0 - qk_i)^2 + Qk_i/4\}. \quad (6)$$

The first three terms represent the contribution of the AA, AA', and $A'A'$ genotypes to the variance attributable to variation in progeny numbers. The fourth term is the binominal variance component due to segregation from AA' heterozygotes, and is independent of the other terms. By definition,

$\sum k_i = N'\mu_k$, where μ_k is the mean number of genes contributed per parent

$\sum k_i^2 = N'V_k + N'\mu_k^2$, where V_k is the variance in number of genes contributed per parent.

Making these substitutions in (6) and using relations (4) we obtain

$$\frac{q(1-q)N'}{2}\{(V_k + \mu_k^2)(1 + F') + \mu_k(1 - F')\}$$

which when divided by $(N'\mu_k)^2$, the square of the total number of contributed genes, gives the variance in the proportion of A genes in the progeny

$$\frac{q(1-q)}{2N'\mu_k^2}\{(V_k + \mu_k^2)(1 + F') + \mu_k(1 - F')\}. \quad (7)$$

However, we are interested only in the variance of the gene frequency increment between parents and offspring, whereas (7) includes the genetic variance of the parent generation. Since the gene frequency change from pool to parent and that from parent to offspring are independent, we can obtain the desired variance by subtracting the parental variance from the offsping variance. Subtracting (5) from (7) gives

$$V_{\delta q} = \frac{q(1-q)}{2N'\mu_k^2}\{V_k(1+F') + \mu_k(1-F')\} = \frac{q(1-q)}{4N}\left[1 - F' + (1+F')\frac{V_k}{\mu_k}\right] \quad (2)$$

where $N(= \frac{1}{2}N'\mu_k)$ is the total number of offspring.

Separate Sexes

If the parental generation is made up of N_m' males and N_f' females, the variance in the change in frequency of genes coming from females is

$$V_{\delta q f} = \frac{q_f(1 - q_f)}{2N} \times \left[1 - F_f' + (1 + F_f')\frac{V_{kf}}{\mu_{kf}}\right] \quad (8)$$

and the formula for genes coming from male parents, $V_{\delta qm}$, is analogous. The total variance in genes from both parents is then

$$V_{\delta q} = \tfrac{1}{4}(V_{\delta q_m} + V_{\delta q f} + 2F\sqrt{V_{\delta q_m} V_{\delta q f}}) \quad (9)$$

where F is a measure of the correlation between uniting gametes due to nonrandom mating. With random mating,

$$V_{\delta q} = \tfrac{1}{4}(V_{\delta q_m} + V_{\delta q f}). \quad (10)$$

When there is no difference in the constants of the female and male parents ($q_f = q_m = q$; $F_f' = F_m' = F'$; $V_{km} = V_{kf} = V_k$; $\mu_{kf} = \mu_{km} = \mu_k$) equation (10) reduces to that for randomly mating monoecious organisms (2).

Polyploidy and Sex-linkage

The formulae may be readily extended to polyploids (Wright and Crow, unpublished) but they will not be derived since the procedures are tedious and the application here is entirely to diploids. For an n-ploid, the formula analogous to (2) is

$$V_{\delta q} = \frac{q(1-q)}{2N}\left\{\left(\frac{1 + (n-1)F'}{n}\right) \times \frac{V_k}{\mu_k} + \frac{n-1}{n}(1 - F')\right\} \quad (11)$$

which reduces to (2) when $n = 2$.

For sex-linked loci, it is convenient to consider male and female offspring separately. For male offspring (in an organism where the male is heterogame-

tic) equation (8) applies (letting N stand for number of male offspring) since the relevant gametes come entirely from the female parent. For female offspring formulas (9) and (10) are correct except that F_m', which of course does not have its usual meaning for hemizygous loci, is considered to have value 1. The variance for female offspring, then, is

$$V_{\delta q_f} = \frac{q(1-q)}{8N_f}\left\{1 - F' + (1 + F') \times \frac{V_{kf}}{\mu_{kf}} + 2\frac{V_{km}}{\mu_{km}}\right\}. \quad (12)$$

The Ratio V_k/μ_k as an Index of Variability

The ratio V_k/μ_k occurs in all the equations derived above and is a measure of the degree of departure from idealized conditions. When $V_k/\mu_k = 1$, as would be the case if the progeny numbers had a Poisson distribution, all the variance formulae reduce to binomial values and the effective number is the same as the actual number of surviving progeny.

We propose, therefore, that this ratio be used as an *Index of Variability* in progeny number. When the value of the index is greater than unity, the effective number is less than the true number; when it is less than unity, the effective number is larger. This ratio has been used by plant ecologists (cf. Clapham, 1936) to measure dispersion in plant locations.

A satisfying feature of the derivations given in the previous section is that no assumptions were made about the nature of the distribution of progeny numbers. In principle the effective number, and the dispersive term in the Fokker-Planck equation, can be determined from the actual number of individuals and the mean and variance of the number of progeny per parent.

Experimental Methods and Results

Three methods were used to determine the index of variability from adult progeny (method I), egg production (method II), and from direct measurement of the sampling variance in gene frequency (method III). All matings were made in shell vials on standard yeast-cornmeal medium. The conditions were sufficiently crowded, so that the mean number of surviving progeny per parent was around 15. A number of mutant and wild type strains were used.

In method I, each vial in a series of replicates was stocked with a number of males (usually 5 or 6) of a multiple recessive stock (e.g., *cn bw*; *e*; *ey*^{2}) and the same number of virgin females, each of a different genotype. The females were all of such types (e.g., *cn*, *bw*, *cn bw*, etc.) that their progeny could be identified. All the parents in any experiment were of the same age, varying from 4–7 days in different experiments. After the vials had been made up they were left undisturbed for several days (usually 3–5, constant for any particular experiment). At this time all vials in which a fly had died were discarded and the flies were removed from the other vials. Offspring were counted for 10 days from the time of first emergence. From 8 to 32 vials were used in each experiment, and the mean and variance in offspring number (μ_{kf}, V_{kf}) were determined for each maternal strain. A large number of such experiments were performed, alike in design but utilizing different markers, leading to a total of 90 analyzable sets of progenies. Another series of experiments with the same design was done with the sexes reversed, to determine μ_{km} and V_{km}. In these experiments 19 sets of progenies ranging from 11 to 35 vials were counted. The summarized results of these experiments are shown in the first and fourth lines of table 1, under the heading "unadjusted," and for separate genotypes in table 3. For detailed results see Morton (1952).

In method II, 5 *cn bw*; *e*; *ey*^{2} males and 5 females of the strain to be tested were placed in a vial containing slants of culture medium with lampblack added to

TABLE 1. *Mean progeny number (μ_k), index of variability (V_k/μ_k), and the ratio of effective number to actual number in Drosophila laboratory experiments by three methods*

	Number of sets of progenies	Unadjusted		Adjusted ($\mu_k = 2$)	
		μ_k	V_k/μ_k	V_k/μ_k	N_e/N
Female parents					
I Adult progeny	90	13.9	4.73	1.82±.09	.71
II Egg production	46	37.2	11.45	1.77±.13	.72
III Gene frequency variance	24	2.0	1.63	1.63±.14	.76
Male parents					
I Adult progeny	19	17.9	11.35	3.18±.37	.48
III Gene frequency variance	14	2.0	4.82	4.82±.77	.35

facilitate counting. Eggs were counted and the parents transferred to fresh vials every 24 hours. The age of the flies, number of replicates, and duration of oviposition were the same as in method I. The means and variances have been divided by the number of female parents to estimate the means and variances of individual egg production. In these experiments 46 sets of eggs were counted. The data are shown in summary on line 2 of table 1 and for individual strains in table 3.

In method III the sampling variance in gene frequency was determined directly for pairs of sex-linked factors, which in different experiments were *f* and f^+, sc^5 and sc^6, and $w^e f$ and w^a (descended from a non-*B* fly in a Muller-5 stock). In order to measure only the sampling variance due to variable numbers of offspring and not that due to segregation from heterozygotes, only homozygous female parents were used and mated with males in such a way that the progeny of each type of female could be identified. Two females of each type (say *AA* and *aa*) were mated with 4 *a* males. The age of the flies and duration of oviposition were the same as in method I. Classification of male and female offspring gave a direct measure of the frequency of the A gene among those contributed by the female parent, and the index of variation could be computed directly from (8). Since there were small but significant

TABLE 2. *Mean progeny number (μ_k), index of variability (V_k/μ_k), and the ratio of effective number to actual number at maturity for Drosophila, Lymnaea, and man*

	Unadjusted		Adjusted ($\mu_k = 2$)		
	μ_k	V_k/μ_k	V_k/μ_k	N_e/N	Source of data
Drosophila					
wild, room temp.	713.8	130.0	1.36	.85	Alpatov
wild, 30°	430.3	153.9	1.71	.74	Alpatov
wild, 19°	941.1	111.4	1.23	.90	Alpatov
wild, underfed	315.5	55.9	1.35	.85	Alpatov
vestigial	432.6	101.5	1.46	.81	Alpatov
Lymnaea	390.9	133.6	1.68	.75	Bailey
Man					
N. S. Wales women	6.2	2.61	1.52	.79	Powys
English women	3.5	2.54	1.88	.69	Pearson
U.S. women, born 1839	5.5	1.28	1.10	.95	Baber and Ross
U.S. women, born 1866	3.0	1.93	1.63	.76	Baber and Ross

changes in gene frequency in most of the experiments, the sampling variance in gene frequency was calculated around the mean gene frequency of the progeny; this removes all but second order effects of selection. A total of 24 sets of progenies was thus analysed, each based on 15 to 32 vials. In all these experiments a random group of four offspring of each sex were counted from each vial; the results are shown in line 3 of table 1. Another series of experiments of the same design was performed with the sexes reversed, to give estimates of μ_{km} and V_{km}. In these experiments, 14 sets of progenies ranging from 9 to 35 vials were counted.

The summary data from these experiments, as tabulated in the first three columns of table 1, show clearly two features. One is that the index of variability, V_k/μ_k, is highly dependent on the mean number of progeny, μ_k. This is discussed in the next section. The second is that in corresponding experiments the index is considerably higher for progeny of males than for progeny of females, as might be expected.

Similar data on lifetime egg production of Drosophila, progeny in Lymnea, and family size in man from other studies are given in the first two columns of table 2.

Age of Enumeration

The formulae developed here are applicable to a situation in which the parents and offspring are enumerated at the same stage of development. Fisher (1939) has shown that the variance is least when the enumeration is made at sexual maturity rather than at some earlier stage. Ideally the index of variability should be determined at this time. In practice this may not be possible, and some procedure is needed to determine from counts made at an earlier stage what the variance would have been had the counts been made at maturity.

As noted earlier, there is a strong correlation between the index of variability and the mean number of progeny per parent. Since in any population that is not expanding or decreasing at a very rapid rate, the average of μ_k counted at sexual maturity cannot be very far from 2, one procedure would be to adjust the value to what it would have been for $\mu_k = 2$. In order to do this it is necessary to make some assumptions as to the manner of survival from young stages to sexual maturity. Two models will be considered.

Model 1. Random Survival

We start out with N families at a certain stage and assume a constant probability, s, of survival to a certain later stage. Let k_{ei} be the number in the ith family at the early stage, e, and k_{ai} be the number at the later (adult) stage, a. The mean number of survivors per family will be $s\mu_{ke}$, where μ_{ke} is the mean number per family at the early stage. The variance of the number per family at the later stage, V_{ka}, is given by

$$NV_{ka} = \sum_{i=1}^{N} (k_{ai} - s\mu_{ke})^2$$
$$= \sum (k_{ai} - sk_{ei})^2 + \sum (sk_{ei} - s\mu_{ke})^2.$$

But, since the distribution of the number of survivors in a family is binomial,

$$\sum (k_{ai} - sk_{ei})^2 = \sum s(1 - s)k_{ei} = Ns(1 - s)\mu_{ke}$$

$$\sum (sk_{ei} - s\mu_{ke})^2 = s^2 \sum (k_{ei} - \mu_{ke})^2 = Ns^2V_{ke}.$$

Therefore,

$$V_{ka} = s(1 - s)\mu_{ke} + s^2V_{ke}. \quad (13)$$

Since s is the probability of survival from stage e to stage a, $s = \mu_{ka}/\mu_{ke}$. Making this substitution, (13) may be rewritten

$$\frac{\frac{V_{ka}}{\mu_{ka}} - 1}{\mu_{ka}} = \frac{\frac{V_{ke}}{\mu_{ke}} - 1}{\mu_{ke}} \quad (14)$$

which shows that the quantity $V_k/\mu_k - 1$ is proportional to μ_k at any stage of development.

Model 2. Survival of the Family as a Unit

The extreme alternative to one of independent survival of the members of a family is that the entire progeny either survives or does not. Using the same symbols as before, the mean number of survivors per family is still $\mu_{ka} = s\mu_{ke}$. The variance in number per (original) family is given by

$$NV_{ka} = \sum_{1}^{sN} (k_i - s\mu_{ke})^2 + \sum_{1}^{(1-s)N} (0 - s\mu_{ke})^2$$

$$= \sum_{1}^{sN} (k_i - \mu_{ke})^2 + \sum_{1}^{sN} (\mu_{ke} - s\mu_{ke})^2 + \sum_{1}^{(1-s)N} (s\mu_{ke})^2$$

$$V_{ka} = sV_{ke} + s(1 - s)\mu_{ke}^2 \qquad (15)$$

and, since $\mu_{ka} = s\mu_{ke}$,

$$\frac{V_{ka}}{\mu_{ka}} + \mu_{ka} = \frac{V_{ke}}{\mu_{ke}} + \mu_{ke}. \qquad (16)$$

These two models lead to quite different results. Whereas with independent survival of progeny the index of variability tends toward unity as the number of survivors decreases, with family unit survival the ratio tends to increase toward $\mu_{ke} + V_{ke}/\mu_{ke}$. There is also a possibility of negative correlations in survival within family units due to intra-brood competition that would lead to departures from model 1 in the opposite direction, but most of the departure from model 1 is likely to be in the direction of positive intra-brood correlations. Presumably, in nature the true situation is somewhere between models 1 and 2. One might expect the situation to be closer to model 1 than to model 2, as there are very few organisms in which the entire lifetime progeny of a parent remain together until maturity, and because intra-brood correlations in survival may be expected to be offset to some extent by intra-brood competition.

In figure 1 the data from table 1 and the Drosophila data from table 2 are graphed to show the extent of the departure from model 1. The scale is proportional to the square root, which does not destroy the linearity of the relationship but permits a wider range of data. The data from females—whether lifetime egg production, short time egg production, adult progeny of females, and adult progeny of females sampled

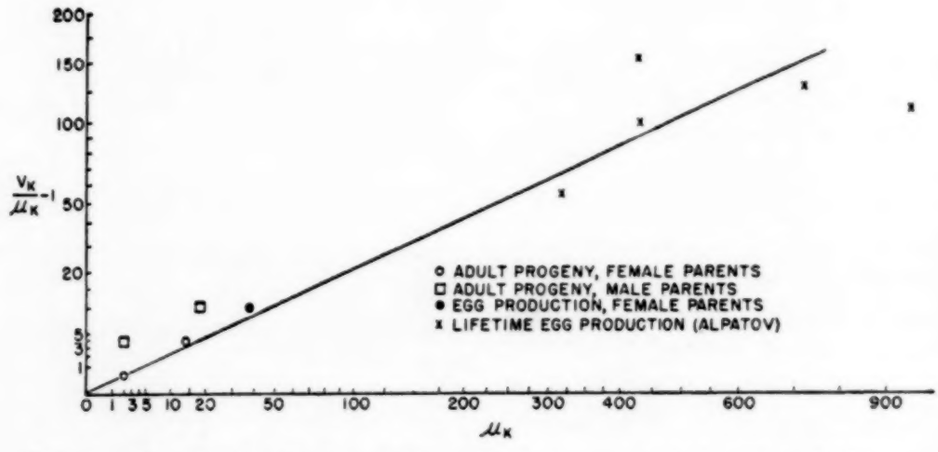

FIG. 1. Graph showing the relationship between the index of variability and the mean number of offspring. Under model 1 (random survival) there should be a direct proportionality between $(V_k/\mu_k) - 1$ and μ_k, and the close fit of the points to this relationship shows the applicability of the model. A square root scale has been used to permit a wider range of data without destroying the linearity of the relationship.

so as to have a mean progeny number of two—all lie very close to the same straight line passing through the origin. This shows that a simple model of random survival applies very well to Drosophila under laboratory conditions, or at least to the genotypes and conditions involved in the experiment. The major factor leading to departure from Poisson distribution in progeny numbers is the original distribution of eggs laid and not differential survival from egg to adult. The graph also shows the sharp difference in variability of males and females in progeny numbers.

If model 1 is assumed to be applicable, it is possible by using equation (13) to adjust the index of variability to the value that it would have if the mean progeny number were reduced to some constant value, e.g., 2. This gives a measure of intrinsic variability in progeny production uncomplicated by correlation with number of progeny produced, and as long as survival is essentially random this would be valid. We have adjusted all the ratios to the value corresponding to a mean progeny number of 2, the appropriate value for a population of stable size. These figures are given in tables 1 and 2 under the heading "adjusted." (The adjusted values in table 1 were not obtained by direct application of equation 13 to the unadjusted values in the table, but rather the adjustment was made in the individual data items before averaging. The reason for this is that the data appear to be more normally distributed after adjustment than before.)

The striking feature of these figures is that, despite tremendous differences in the index of variability in the various organisms at various stages, the index for offspring of females of all the species is between 1.23 and 1.88 when adjusted and the effective number, as defined by (3), is between 70 and 80 per cent of the actual number.

Index of Variability in Different Strains

The conclusions thus far presented concern relationship between index of variability at various stages of development and the relative constancy of these for various organisms and strains under various conditions when they are adjusted to the same mean number of progeny. In addition there is a second order effect of another type. Table 3 shows the index of variability, unadjusted and adjusted, for various strains at the same stage. These data show a small, but significant, inverse relation between the index of variability and the average number of progeny. This relation is shown graphically in figure 2.

When compared within a stage and

Table 3. *Mean progeny number* (μ_k), *index of varability* (V_k/μ_k), *and adjusted index* (V_k/μ_k; $\mu_k = 2$) *for various Drosophila stocks*

	μ_k	V_k/μ_k	$V_k/\mu_k;\mu_k=2$
Female parents			
Adult progeny			
dp	7.2	6.360	2.499
In(1)sc^{8}w^{a}	7.4	7.287	2.699
cn bw;e;ey^{2}	9.3	4.049	1.656
dp cn bw;e;ey^{2}	9.3	8.240	2.553
B	11.7	3.171	1.372
bw	13.0	6.417	1.835
sc^{5}, sc^{6}	13.9	6.307	1.762
cn	17.8	5.810	1.541
cn bw	18.3	3.054	1.224
Mass. 38	19.5	3.354	1.241
Egg production			
cn bw;e;ey^{2}	19.7	12.121	2.131
dp	21.8	35.305	4.154
cn	36.3	10.955	1.549
bw	37.7	14.209	1.701
dp cn bw;e;ey^{2}	41.2	5.832	1.235
cn bw	44.8	10.592	1.429
Male parents			
Adult progeny			
dp cn bw;e;ey^{2}	2.2	6.590	6.130
cn bw	5.1	9.220	4.200
cn bw;e;ey^{2}	6.8	11.390	4.056
bw	8.2	9.542	3.096
B	9.0	9.670	2.937
cn	25.1	14.298	2.058
f	45.1	12.240	1.499

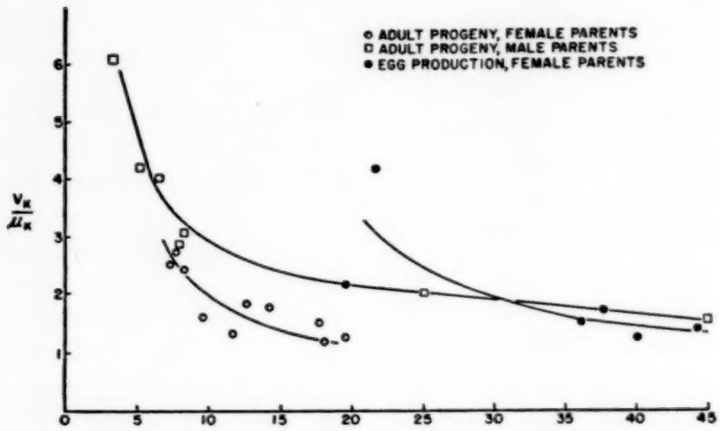

FIG. 2. Graph showing the relationship between the adjusted index of variability and the mean number of progeny for different strains of Drosophila. For different strains counted at the same state there is a negative relationship between the index of variability and the mean. Curves drawn by eye.

sex, there is a clear tendency for those types of parents producing the largest numbers of offspring to have a smaller adjusted index of variability in offspring production. The trend holds for egg production and for adult progeny of males and females.

THE PROGENY NUMBER DISTRIBUTION

In the analysis so far there has been no discussion of the form of the distribution of progeny numbers; in fact, it is a virtue of the method that no assumption as to the form of the distribution is needed.

However, in the actual analysis of populations in nature it may be necessary for some purposes to describe other properties than the mean and variance of progeny numbers. If a distribution is to be used, a desirable property is that the form of the distribution not change in going from an early stage to a later one by random survivals. Fisher (1939) has shown that this is true if the progeny have a Poisson distribution.

However, this property is by no means confined to the Poisson distribution. The negative binomial or Pascal distribution has found wide application in this type of problem. It, too, among others has the property of functional invariance with random survival as can be quickly shown by the use of generating functions. The generating function of the negative binomial is

$$g(s) = \left[\frac{1 - c}{1 - cs}\right]^r$$

while that of the binomial is $f(s) = q + ps$. The generating function of the compound distribution is $g[f(s)]$ (see Feller, 1950, p. 222), which in this case is equal to

$$\left[\frac{1 - c}{1 - c(q + ps)}\right]^r = \left[\frac{1 - \frac{cp}{1 - cq}}{1 - \frac{cp}{1 - cq}s}\right]^r$$

which is the generating function of the negative binomial with parameters r and $cp/(1 - cq)$. Thus, in our case, a population originally distributed as a negative binomial would, after random survival, still be distributed in the same form with one parameter remaining the same and the other being a function of the original parameter and the proportion of survivors. For a discussion of this and related topics in population ecology, see Skellam (1952).

Under some circumstances the presence of a class of parents with zero offspring may be troublesome. If the

typical number of offspring at some stage is very large, or even otherwise, the presence of an appreciable zero class could lead to a distribution that is bimodal. From the standpoint of assessing the role of drift due to small population number this is not important, but if a distribution is to be fitted this is a serious handicap. One way of avoiding this problem is to enumerate only fertile adults, counting those that reach sexual maturity but do not reproduce as among the non-survivors.

Discussion

In natural biparental populations μ_k cannot be far from 2 without the population increasing explosively or quickly becoming extinct. We have shown that as long as there is a stage of random survival intervening between the stage of enumeration and sexual maturity, the index of variability (adjusted to $\mu_k = 2$) is of the order of unity even if the value was much larger at an earlier stage. For example, in an organism with a mean progeny number at birth of 10^3 with a variance of 10^6 (variability index = 1000), the adjusted index is about 3. Thus any population to which this model applies will not have an effective number greatly different from the number of breeding adults.

This study has also shown that in laboratory Drosophila cultures model 1 (random survival beyond the enumerated stage) is consistent with the results obtained. We are impressed with the way in which the values for adult offspring of females and egg production lie close to the same line in figure 1, despite the variety of strains and experimental procedures used. Alpatov's data were for lifetime production of eggs obtained by periodic transfers of the parents to new media. Our egg data were from eggs laid over a 3–5 day period under quite different cultural conditions. The adult progeny were obtained from cultures crowded enough to result in considerable mortality. Alpatov's data include variance due to differing length of life, but since the egg production falls off decidedly in later life it is likely that the total egg production is more constant than might be expected from variance in daily production and longevity.

One can only guess at how well this model fits in nature. In most organisms there is probably some intra-brood correlation in fate because of the close association of a brood in time and space. A clutch of bird eggs or a group of eggs laid by a parasitic wasp on a single caterpillar are quite likely to survive or die as a unit. Also, in so far as genetic factors affect survival there would be some correlation within progenies because of genetic similarity. However, it seems to us quite doubtful that there are many species in which there is even approximate approach to a model in which the lifetime progeny of a parent survive or die as a unit. Nonetheless, and despite the possibility of some intra-brood competition, it seems likely to us that many populations depart from model 1 somewhat in the direction of model 2. Model 2 may be more-or-less applicable during the early part of the progeny development and model 1 at a later period.

As an illustration consider a population in which the average number of progeny per parent at birth is 100 and the variance is 5000, so that the index of variability at birth is 50. If survival is entirely at random the adjusted index ($\mu_k = 2$) is 2 and the effective number (by equation 3) is 2/3 the actual number. If the pattern of survival is such that the progeny average is reduced from 100 to 50 by the death of entire progenies and from that time on is at random, the adjusted index is about 5, and the effective number is 1/3 the actual number. If the initial death by entire progenies is enough to bring the average down to 20 per parent, the adjusted index is about 14 and the effective number about 2/15 the actual number. This is an extreme model in that is assumes that the entire

progeny of a parent survive as a unit for a part of the developmental period. We believe that only very unusual conditions could result in the actual and effective numbers differing by as much as an order of magnitude, and that usually they are much more similar. Fortunately, this is a point capable of direct study in natural species, for example in game animals, where detailed studies are feasible or in birds where progeny may be identified by banding.

The data from tables 1 and 2 show another point. We find the similarity of the adjusted index values in the three species, Drosophila, Lymnea, and man very striking. By this criterion females of Drosophila, Lymnea, and Homo are very similar in their intrinsic variability in progeny number; the adjusted variability index is in the vicinity of 1.5–1.75 corresponding to an effective number about 3/4 the actual number of breeding adults.

Our results are in substantial agreement with other studies on laboratory Drosophila. Prout (1954) measured the allelism of lethals from a population that had been irradiated for many generations and had apparently reached equilibrium of numbers of lethals. The actual number of adults fluctuated around 1000. By assuming the population is at equilibrium and making a few other necessary simplifying assumptions Prout estimated the effective number as about 250, though this figure is subject to a large error. The population size was not constant, and the effective number should be related to the harmonic mean which may be less than 1000. Kerr and Wright (1954) studied the rate of fixation of sex-linked alleles (forked and non-forked) in an artificial population of exactly 4 males and 4 females maintained over several non-overlapping generations. They estimated the effective number to be 83 per cent of that expected in an idealized population. All three studies agree in showing an effective number less, but not greatly less, than the actual number.

The analysis of our results broken down into different genotypes showed a definite tendency for the parents that produced larger numbers of progeny to produce more constant numbers. Dobzhansky and Wallace (1953) have discussed the phenomenon of "homeostasis" in relation to heterozygosity. Several studies in Drosophila (Wigan, 1944; Robertson and Reeve, 1952) and elsewhere (e.g., Grunberg, 1954) have also shown a greater constancy of expression in heterozygotes than in homozygotes. It has long been recognized in corn that inbred lines are quite variable as compared with first generation hybrids. To what extent this constancy is a consequence of heterozygosity *per se* or to the higher adaptive level of the heterozygotes is not known. If a comparison is justified, our data suggest that some homeostasis may be a consequence of a high level of fitness, since there is no reason to think that our high producing strains are any more heterozygous than the low producing.

The effective number used in this article is related to the magnitude of the sampling variance in gene frequency from generation to generation. It is also possible to define effective population in terms of the probability of randomly chosen genes having been descended from a common ancestor (Wright, 1939). The two concepts lead to practically the same conclusions when the average number of progeny per parent is 2 or when the ratio V_k/μ_k is equal to 1; in other situations they are different, and under some circumstances may be strikingly different (Crow, 1954). Our formulae are also in agreement with Haldane (1939) for the case $\mu_k = 2$, $F' = 0$. We have chosen a definition based on variance since this is the quantity directly related to the Fokker-Planck equation.

The mathematical theory developed by Wright and others assumes that the population number remains constant, or is a deterministic function of time.

Wright has pointed out (1939 and elsewhere) that the effective number over a period of time is approximately the harmonic mean of the individual values. More exactly,

$$\frac{1}{N_e} = 1 - \left[\prod_1^t \left(1 - \frac{1}{N_i}\right)\right]^{1/t} \sim \frac{1}{t}\sum_1^t \frac{1}{N_i}$$

(Crow, 1954).[2] The theory has not yet been developed for the situation where the population number is a probabilistic function (Feller, 1951).

The fact that this study deals only with the results of a small population number is not intended to imply that this is the only, or even necessarily the major factor in the determination of $V_{\delta q}$ in nature. Variability in migration and selection coefficients have effects that are superficially very similar and may be more important (Wright, 1935, 1948; Fisher and Ford, 1947, 1950; Kimura, 1954). But in an organism with genes of the order of 10^4 and producing 10^1 or 10^2 progeny per parent, and considering the amount of purely accidental survival, there may very well be a large number of genes on which selection is acting with very little intensity, and which could be subject to considerable drift in a small population.

The evolutionary significance of $V_{\delta q}$, whether due to small population number or to variable coefficients, has been developed fully by Wright (for recent reviews see 1948, 1949, 1951; but cf. Fisher and Ford, 1947, 1950).

Summary

The process of gene frequency change in a population is adequately described by the Fokker-Planck equation and the only measurements needed are the mean systematic increment per generation, $M_{\delta q}$, and the mean square change due to dispersive factors, $V_{\delta q}$. It is shown that, for a randomly mating diploid population,

$$V_{\delta g} = \frac{q(1-q)}{4N}\left[1 - F' + (1 + F')\frac{V}{\mu_k}\right]$$

where q is the gene frequency, F′ is the inbreeding coefficient of the parent generation, N is the total number of progeny, and V_k and μ_k are the variance and mean of the number of progeny per parent. Formulae are also given for sex-linked and polysomic loci.

We suggest that the ratio V_k/μ_k be used as an *index of variability* in progeny number; when the ratio is one the effective number is equal to the actua. number, when the ratio is greater than one the effective number is smallerl Formulae are given for converting the index measured at an early stage in development to any later stage on either of two models: (1) random survival, and (2) survival or extinction of each family as a unit. The data on laboratory Drosophila fit much more closely to model 1. When adjustment is made on this model the ratio of effective to actual number as measured in three kinds of experiments was .71, .72, and .76 for progeny of female Drosophilae; for progeny of males the ratio was .48 and .35 by two methods.

Data from female parents in Drosophila cultures, Lymnea, and humans all show a ratio of effective to actual number between .7 and .95. We conclude that only under rather unusual conditions would the effective number be of a different order of magnitude than the actual number.

Acknowledgment

We should like to thank Mr. Motoo Kimura and Professor Oscar Kempthorne for providing alternative derivations of equation (2). We are especially indebted to Professor Sewall Wright for help in deriving equations (2) and (11) and for many stimulating discussions and helpful suggestions.

[2] We should like to correct an error in this article. The top two formulae on page 549, stated to be only approximately equal, are in fact exactly equal.

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NOTES AND COMMENTS

HOMOLOGOUS EYE COLOR MUTANTS IN THE HONEYBEE AND DROSOPHILA

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The eyes of probably all insects contain, as a major component, a brown pigment first called ommatin and more recently renamed insectorubin (Goodwin and Srisukh, 1950). As a result of investigations of the eye color mutants vermilion (*v*) and cinnabar (*cn*) in *Drosophila melanogaster* and the *a* color mutant in *Ephestia kuhniella*, the first stages in the biosynthesis of insectorubin have been described. (See Ephrussi, 1942; Beadle, 1945; and Caspari, 1949 for reviews of the literature.) It has been demonstrated that dietary tryptophan is the immediate precursor of insectorubin. The formation of insectorubin follows after tryptophan has been oxidized sequentially to the intermediate compounds formylkynurenin, kynurenin and oxykynurenin as well as, in all probability, several additional unknown intermediates. Mutants which block these first stages in the biosynthesis of insectorubin can be characterized by a number of criteria. The *v* and *cn* mutants in *D. melanogaster* serve to illustrate these criteria. Insectorubin synthesis fails in the presence of either mutant. Studies of genetic mosaics and/or transplantation experiments demonstrate that both mutants are developmentally non-autonomous thereby differentiating *v* and *cn* from other eye color mutants. The *v* flies fail to oxidize tryptophan which they accumulate (Green, 1949) but can synthesize insectorubin when exogenously supplied with formyl-kynurenin or kynurenin. The *cn* flies fail to oxidize kynurenin which they accumulate (Kikkawa, 1941; Green, 1949) but can synthesize insectorubin when exogenously furnished with oxykynurenin. By utilizing these criteria it is possible to demonstrate that parallel mutants occur not only in other Drosophila species but in other insect species belonging to other orders as well. Thus in the Lepidoptera the *a* mutant of *Ephestia kuhniella* parallels *v* of Drosophila (Caspari, 1949) and the *w*-1 mutant of *Bombyx mori* parallels *cn* of Drosophila (Kikkawa, 1941), while in the Hymenoptera the *o* and o^1 mutants in *Habrobracon juglandis* parallel *cn* of *D. melanogaster* (Beadle *et al.*, 1938).

Recently, a number of eye color mutants in the honey bee, *Apis mellifera*, have been described (Rothenbuhler *et al.*, 1953a; Laidlaw *et al.*, 1953). The genetic information indicates that all eye color mutants are inherited independently of each other. Two mutants, snow (*s*) and ivory (*i*), are of special interest since in both of these the eye pigment is completely absent resulting in a white eye phenotype. (On the basis of solubility and spectral analysis, the bee eye pigment is insectorubin.) Moreover, both the *s* and *i* mutants have been described as developing non-autonomously in mosaics (Rothenbuhler *et al.*, 1953b). These facts suggest that the *s* and *i* mutants are homologues of *v* and *cn* of Drosophila, i.e., block the same steps in the biosynthesis of insectorubin.

As a first step in establishing the homology, analyses of the non-protein tryptophan content of *s* and *i* worker bees were made. Adult workers were collected within 24 hours after emergence and lyophillized. Tryptophan analyses were made using methods previously described (Green, 1949). The following results, expressed as mean mg. non-protein tryptophan per gram of dry adult worker, were obtained: *s* workers, 1.87 mg. (range 1.79–1.930); *i* workers, 0.79 (range 0.75–0.82). Thus the *s* workers accumulate non-protein tryptophan not unlike the accumulation in *v* Drosophila, whereas *i* workers do not. Since *i* is non-autonomous, it could be reasoned that while no accumulation of tryptophan occurs, *i* acts biochemically like *cn* of Drosophila and accumulates kynurenin or acts like the *w-2* mutant in *Bombyx mori* which accumulates oxykynurenin (Kikkawa, 1953).

The accumulation of kynurenin or oxykynurenin can be detected by feeding lyophillized *i* workers to *v* and *cn* larvae of *D. melanogaster*. If kynurenin is present, it will be utilized by *v* larvae in the biosynthesis of insectorubin but not by *cn* larvae. Accordingly the eyes of the emerging *v* adults will be pigmented, those of *cn* adults will not. If oxykynurenin is present, it will be utilized by both *v* and *cn* larvae and the eyes of both types of emerging adults will display pigment. As controls, larvae were raised on unsupplemented media, and *v* larvae were raised on media supplemented either with *s* workers or with adult *cn D. melanogaster*.

The feeding technique has been previously described (Green, 1952). A lyophillized bee or Drosophila supplement weighing 250 mg. was added to the two ml. of media. The results of the feeding experiments are tabulated in table 1.

These experiments demonstrate that *i* workers like *cn* individuals of Drosophila accumulate kynurenin as indicated by the formation of

TABLE 1. *Bioassays for the detection of kynurenin and oxykynurenin*

Supplement added to 2 ml. media	Genotype host larvae	Eye pigments[1] emerging adults
none	*v*	0
i workers	*v*	2.0–3.0
s workers	*v*	0
cn (D. melanogaster)	*v*	1.0–2.0
none	*cn*	0
i workers	*cn*	0

[1] Arbitrary scale of pigmentation. No insectorubin = 0, maximal insectorubin (as in wild-type) = 5.

insectorubin when *i* is fed to *v* larvae and the lack of pigment when supplied to *cn* larvae. These experiments also confirm the observation that in *s* workers tryptophan is not oxidized but merely accumulates. From these observations it can be concluded that the *s* mutant of the honey bee is homologous to the *v* mutant of Drosophila and to the *a* mutant of *Ephestia kuhniella*, while the *i* mutant of the honey bee is homologous to the *cn* mutant of Drosophila, the *o* mutant of Habrobracon and the *w*-1 mutant of Bombyx.

Is it possible that the several eye color mutants described here as being homologous represent identical mutations occurring in rather widely separated insect species? There are suggestions that this may indeed be the case. There are a number of ways by which the oxidation of kynurenin to oxykynurenin could be blocked. Presumably different biochemical blocks of this oxidation would be the consequence of non-allelic mutants. However, the available data indicate that the same *cn* mutation occurs in a number of Drosophila species (Sturtevant and Novitski, 1941), and therefore not several but only one of the possible biochemical blocks in the oxidation of kynurenin is realized. The widespread occurrence of the same *cn* mutation in Drosophila suggests that this same mutation occurs in the honey bee as *i*, in Bombyx as *w*-1 and in Habrobracon as *o*. Similar considerations suggest that *v* of Drosophila, *a* of Ephestia and *s* of the honey bee all represent the same mutation. These suggestions are supported by the fact that the mechanism of insectorubin synthesis appears to be the same in all these species. Considered together, these facts point to the conclusion that the genic material controlling insectorubin synthesis is common to the different insect species considered, and that this genic complex was probably derived unaltered from a common ancestral form.

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THE CORAL SNAKE "MIMIC" PROBLEM AND PROTECTIVE COLORATION

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INTRODUCTION

In a recent paper in this journal Dunn (1954) restated the old problem of mimics vs. protective coloration in coral snake "mimics." He suggested that if he could show that there were more poisonous coral snakes than non-poisonous "mimics" in a random population (Panamá), the case for these non-poisonous snakes being true "mimics" would be established for the many diverse types of colubrid snakes which have become coral snake-like in their coloration.

Dunn's data are to the effect that " . . . a minority (38%) of the conspicuously ringed snakes are relatively or quite innocuous. These individuals represent nine species, seven genera, and three subfamilies. A majority (68%) of such snakes are very definitely venomous. These individuals represent six species, all of the same genus, *Micrurus*."

Other than mentioning a few references, Dunn did not discuss the other aspect of the problem, namely that of protective coloration. It is the purpose of this note to attempt to show that a simpler solution of the problem is achieved by considering the coral snake *and* its "mimics" to be cases of convergent evolution of protective coloration, both concealing (disruptive) and deflective (illusion effect).

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COLORATION IN SNAKES

Next to changes in body proportions and development of poison apparatuses in snake evolution (Schmidt, 1950), the most important or conspicuous diversification of snakes seems to have been in color and color pattern. In general the major color patterns of snakes are (Schmidt and Davis, 1941; Klauber, 1931):

Blotched (including spotted, mottled, or diamonds): This type of pattern is usually found in large, slow-moving snakes or in snakes which depend primarily upon concealing coloration for protection from predators. The ground color and the blotches usually blend in with the background coloration. (Ex. *Boa*,[1] *Crotalus, Bothrops, Lachesis, Pituophis, Leptodeira, Trimorphodon, Heterodon, Epicrates, Bitis,* and probably *Dipsas, Sibon,* and *Imantodes.*)

Uniform: This type of coloration is usually found in burrowing or secretive snakes (Ex. *Leptotyphlops, Geophis,* most *Tantilla, Carphophis,* and *Diadophis*), in relatively swift snakes (Ex. *Masticophis flagellum, Coluber constrictor, Ptyas*), or in snakes found in an almost uniformly colored habitat (Ex. *Leptophis, Oxybelis, Opheodrys,* and to some extent, *Coluber constrictor*).

Striped: Stripes are usually found in fast-moving slender snakes. It usually contributes to the optical illusion (to man, at least, and probably to the snake's predators as well) of having the stripes coming closer together as the snake proceeds through the grass, brush, or rocks. The eyes become focused on the stripes and do not follow the snake forward as it moves, but instead the focus of the eye moves posteriorly as the snake passes. The effect is that the stripes become closer together, meet at a point, and then are gone. While the eye stays fixed at the ground for a moment, the snake has moved on ahead and is lost to the predator (Klauber, 1931; Schmidt and Davis, 1941, p. 33). (Ex. *Salvadora, Masticophis lateralis, M. taeniata, M. bilineatus.*) When these snakes are concealed—as in the base of a bush—the stripe may aid in disruptive coloration, as any person who has chased one of these snakes through a mesquite bush well knows.

Banded (cross-bands, rings): Bands on a moderately fast-moving snake have the same effect as do the stripes. The eyes become focused on a series of bands and shift along the bands as they become smaller and smaller until the snake is gone. That this illusion effect is similar to the effect of the stripes (to man, at least, and probably the snake's predators as well) is well impressed on any collector who has chased a banded snake through the brush. The bands also aid in disruptive coloration for a snake in concealment or partial concealment while foraging. (Ex. *Lampropeltis g. getulus, L. g. californiae*-ringed phase, *L. doliata, L. pyromelana, L. zonata, Micrurus, Micruroides, Notechis, Rhinocheilus, Sibynophis venustissimus, S. zeteki, Pliocercus euryzonus, Erythrolamprus bizona, E. mimus, Chionactis,* etc.)

Hence the basic color pattern in snakes seems to be toward some type of protective coloration.

[1] Most of the examples are from the New World, others could be obtained for other parts of the world by going through the standard herpetological texts for each area.

Protective Coloration in Banded Snakes

Typical Banded Snake: As has been described above, protective coloration is achieved by a banded snake, Ex. *L. g. getulus,* in two ways. First by an optical illusion effect (a deflective effect) while moving through brush, rocks, etc., in the decrease in size of the bands as the snake proceeds, and second by disruptive coloration, or breakup of the outline of the snake in concealment or while moving slowly in search of food.

Red, yellow, and black-banded snake: The condition of protective coloration of a bright colored snake such as a coral snake or any of its "mimics" is, in reality, probably no different from that of a typical banded snake. The only difference is the presence of red. The effect to the predator is the same, for example:

Night: Most coral snakes and their "mimics" are nocturnal (Dunn, 1954). At night colors are differentiated with difficulty, if at all, by animals that have color vision and hence the red appears black or gray. In bright moonlight some color can be detected by some human beings. In the absence of the moon, color is probably impossible to discern. Most of the coral snakes and their "mimics" live in tropical jungles or in forested areas where the moonlight seldom penetrates the forest floor. Those coral snakes and their "mimics" that live in open country seem to have a reduced activity during moonlight nights (Klauber, 1931). Rodent activity is also definitely reduced on moonlight nights in open country (as is well known to mammalogists) and rodents are the primary source of food for the "mimics." Predator activity may also be reduced on moonlight nights in open country.

To color-blind animals the effect at night is the same, red appears black or gray. Hence at night, the banded coral snake and its "mimics" are no different from any banded snake. It is protectively colored by disruptive coloration while quiet or slowly moving or by the illusion effect when moving fast.

It is interesting to note here that the supposedly conspicuously colored, primarily nocturnal, sand dweller, *Chionactis occipitalis,* which is so well adapted to sand dwelling, has been shown to climb into creosote bushes in natural and escape behavior (Warren, 1953). The banded effect (red, black, and yellow—gray, black, and light at night) blends in extremely well with the dark nodes and light internodes in the branches of the creosote bush (Warren, 1953, p. 123).

Day: In the daytime, to a color-blind predator (most snakes and other predators on these snakes are probably color-blind, Walls, 1942; Cresitelli, personal communication and MS), the coral snake and its "mimic" still appears black and white, or black, gray, and white. It is thus probably just as difficult to see and the illusion effect the same, as in a typically banded snake.

To a color sensitive predator (what few there are) the red probably intensifies the illusion effect described above and the only difference is that red, yellow, and black bands are passing by in front of the predator instead of just black and yellow bands.

Mimics

Undoubted mimicry occurs in many groups of animals (Thayer, 1918; Cott, 1940). For example, bee-flies (Diptera-Bombycillidae) are almost perfect mimics of bees (Hymenoptera-Apidae, Megachilidae, and Anthophoridae). In general, where true mimicry occurs it is monophyletic in origin and a whole family or genus mimics another group or species.

Convergence in Protective Coloration

Most supposed "mimics" probably represent convergent evolution of protective coloration. In regard to coral snakes and their "mimics" this appears to be true, as:

1. The basic evolution of pattern of snakes seems to be towards or maintaining protective coloration.

2. This seems to explain why many different and diverse groups of snakes have evolved the same type of pattern. "Mimics" have developed in several subfamilies of colubrids and may be at present evolving in others (Ex. *Scaphiodontophis,* Taylor and Smith, 1943).

3. This explains why so-called "mimics" occur in areas where no coral snakes occur (Ex. *Lampropeltis zonata* and *L. doliata* in North America). More important, it explains why "coral snake"-like colored snakes occur in Europe, Asia, and Australia. Standard works on these areas show the following snakes to have red and black, or red, black, and yellow rings, bars, or bands: *Boiga forsteni, B. ochracea, Oligodon cyclurus, O. albocinctus, O. cinereus, O. arnensis, Calamaria semiannulata, Dipsadomorphus drapiezii, Demansia n. nuchalis, Rhynochoelaps b. bertholdi, Callophis macclellandi, Coluber porphyraceus.* In addition, the following Old World forms have red in some pattern (spots, etc.) on the dorsum: *Elaphe leopardina, Coluber hippocrepis, Plectrurus guentheri, Uropeltis maculatus, Oligodon bitorquatus.*

This also helps to explain why further evolution of color pattern has occurred in some forms after the "mimic" coloration has been evolved (Ex. *Lampropeltis zonata,* Zweifel, 1952).

The presence of red in snakes in the first place may result from excess carotinoids in

metabolism or some physiological blockage (through gene control) of some process preventing excretion or elimination of carotinoids (see Fox, 1953).

4. This helps to explain why not all phases of coral snake patterns (Ex. Triad, Dunn, 1954) are mimicked and perhaps why the arrangement of colors is different in the many forms of coral snakes and coral snake "mimics."

5. The effect of protective coloration, whether concealing (disruptive) or by optical illusion effect (deflective), is probably achieved equally well (see above) by bands whether two or several colors are used. This is especially true if most of the predators are color-blind (red appearing black or gray) and/or nocturnal, and is intensified (for the illusion effect) if the predator has color vision in the daytime.

6. Most coral snakes are snake-eaters (Dunn, 1954) and hence would probably consume any snakes of proper size that they came upon. That a snake happened to be a red, black, and yellow "mimic," would probably mean little to the apparently color-blind coral snake. If it was, in fact, another coral snake, the proper sex discriminating releasers would probably be elicited and courtship or aggressive behavior (depending upon the sexes) would result (see Shaw, 1951, for a discussion). If the wrong behavioral responses for sex and species identification were given by a "mimic," the predaceous coral snake would probably respond by consuming its own "mimic."

7. It seems easier to explain that various groups of snakes have evolved a similar color pattern that is of a protective nature by normal means of natural selection, than to suggest several independent evolutionary attempts at mimicry of a relatively unimportant poisonous snake (as far as total fauna is concerned—not as far as man is concerned). In Dunn's sample, 5.5% of the total species of snakes collected were coral snakes and these represented only 5.2% of the total number of individual snakes caught (Dunn, 1949, 1954).

The mimicry theory depends on the survival of an individual predator after a coral snake bite. Most mammals would probably die from most coral snake bites. Most hawks and owls seem to escape injury from poisonous snakes, when they do eat them, due to their method of grabbing, flying, and killing and hence will continue to kill and eat coral snakes and their "mimics." A record in point is of an adult, uninjured, laughing falcon (*Herpetotheres achinnans*) collected in Nicaragua containing an adult *Micrurus*, without a head, in its stomach (Howell, MS). The predator, if it was bitten and survived, would have to remember this experience the next time it came upon a red, black, and yellow snake. In the case of true mimics, the harmful effect of the poisonous animal mimicked is not great. As a result, the predator can learn the result of the poison or sting and remember it the next time it sees a similar colored animal (Ex. Cott's (1936) experiments with toads and bees). It is also difficult to see how such a learned relationship or idea in the mind of the predator, if it survives the bite, is to become inherited.

It is therefore suggested that not only coral snake "mimics," but the coral snakes as well, represent convergent evolution of pattern toward increased protective coloration either by concealment (by a disruptive pattern) or by intensifying the optical illusion effect (by a deflective effect) of most banded snakes.

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